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Knuckle-Walking Signal in the Manual Phalanges and Metacarpals of the Great Apes (Pan and Gorilla)

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KNUCKLE-WALKING SIGNAL IN THE MANUAL PHALANGES AND METACARPALS OF THE GREAT APES (*PAN* AND *GORILLA*)

A Dissertation Presented

By

STACEY ANN MATARAZZO

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ABSTRACT

KNUCKLE-WALKING SIGNAL IN THE MANUAL PHALANGES AND METACARPALS OF THE GREAT APES (*PAN* AND *GORILLA*)

MAY 2013

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The "Knuckle-walking Hominin Hypothesis" postulates that there was a knuckle-walking phase during the transition from quadrupedalism to bipedalism. To address this question, previous research has focused on the search for a "signal" within the wrist, and metacarpals of extant knuckle walkers that can be used to infer this locomotor pattern in extinct hominins. To date, the examined features have not yielded a clear, non-contested signal. I explore the Knuckle-walking Hominin Hypothesis in two ways: 1. by examining the hand postures and the manual pressure application of *Pan* and *Gorilla* during knuckle walking to determine whether there are species specific differences and 2. by examining the internal and external morphology of the manual phalanges in an attempt to isolate a clear "knuckle-walking signal". Chimpanzees are more variable in their preferred contact digits, and use both hand positions with equal frequency ("palm-in" - palm facing toward the body and "palm-back" - palm facing posteriorly). In contrast, gorillas consistently make contact with all four digits 2-5, maintain a pronated arm, and use the palm-back hand position. In both taxa, hand position affects which digit acts as the final touch-off element and therefore receives maximum pressure in a given

step, and digit 5 receives significantly less pressure than the other rays. Gorillas are, in effect, practicing a refined subset of the variety of knuckle-walking postures used by the more arboreal chimpanzees.

A clear knuckle-walking signal is seen in both the external and internal morphology of the phalanges. Chimpanzees and gorillas have the same middle phalangeal curvature profile with the greatest curvature found in digit 5 (5 > 2 > 3 > 4), the element that receives the least amount of pressure. This phalangeal curvature profile is a feature not shared with any of the included taxa practicing different modes of locomotion. They also have similar Indices of Relative Curvature (IRC-middle phalangeal curvature/proximal phalangeal curvature) for digits 2-5 that clearly delineate them with "flatter" middle phalanges and more curved proximal phalanges (IRCs = ~0.85), from quadrupeds with more curved middle than proximal phalanges (IRCs > 1), and suspensory primates with higher and more equal curvature values for both elements (IRCs = ~1). This ability to differentiate between locomotor groups holds if the IRCs are composed of elements from different rays of the same manus and from elements of different individuals. Within the trabecular bone structure, knuckle walkers are differentiated from quadrupeds and suspsensory primates in 3 locations: the metacarpal head, and the proximal ends of the middle and proximal phalanges. In particular, the metacarpal head shows distinct differences between the groups: knuckle walkers have a palmar-dorsal alignment of trabeculae and disc-like shape, suspensory taxa have a proximodistal alignment and rod-like shape and quadrupeds have a proximodistal alignment and disc-like shape. The ability to differentiate between locomotor categories

using isolated zones increases the applicability of these signals to a fragmentary and limited fossil record. The morphological similarities, specifically the shared curvature profile, and the similar knuckle-walking kinematics employed by chimpanzees and gorillas point to a shared origin of knuckle walking.

PREFACE

The main body of this dissertation consists of three chapters (2-4) each constructed in a publishable paper format bordered by introductory and conclusion chapters. Each chapter contains its own introduction, methods, results, discussion, and conclusion segments. The introduction for chapter three "Manual Phalangeal Curvature and Knuckle walking in African Apes" was largely borrowed from my earlier work on phalangeal curvature published in 2008 which is cited throughout.

Chapter 2 presents research involving animal participants. Pressure application to the manus was collected when chimpanzees and gorillas knuckle walked across a pressure mat installed within their respective enclosures. This work was approved by Animal Care and Use Committees at the University of Massachusetts, Amherst (IACUC # 2010-0006), the Lincoln Park Zoo, Chicago, IL, the Franklin Park Zoo, Boston, MA, and the Cognitive Evolution Group, University of Louisiana at Lafayette, LA. The project was designed with the input of the animals' primary handlers to inflict minimal interruption to the daily routines of the animals and their keepers. Animals were able to cross the pressure mat at will and avoid it if they chose to, thereby minimizing stress to individual animals.

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CHAPTER 1

INTRODUCTION: THE KNUCKLE-WALKING HOMININ HYPOTHESIS

History of the "Knuckle-walking Hypothesis"

The nature of the hominin transition to bipedalism has been widely debated. Did our pre-hominin ancestors have a knuckle-walking phase, or was another form of quadrupedalism or suspension the primary mode of locomotion? Within the subfamily Homininae (*Pan*, *Gorilla*, and *Homo*), *Pan* and *Homo* form a lineage that diverged from *Gorilla* approximately 8.3million years ago (Perelman et al., 2011). If knuckle walking is deemed to be ancestral to the Homininae lineage, then it implies that hominin ancestors went through a knuckle-walking transitional period. The knuckle-walking hypothesis which reconstructs the ancestor as being adapted to knuckle walking and arboreal climbing, is widely supported (Begun, 1993; Corruccini, 1978; Inouye and Shea, 2004; Kelly, 2001; Richmond and Strait, 2000; 2001a; 2001b; Richmond et al., 2001; Shea and Inouye, 1993; Washburn, 1967; 1968), but it is just one of several hypothesis posited to explain the origin of bipedalism. The others hypothesize that the ancestral condition was a more "monkey-like" arboreal or terrestrial quadrupedalism, a more "orangutan-like" or "gibbon-like" climbing and suspension, or a more generalized arboreal ape condition not seen in extant primates (Gebo, 1996; Morton, 1926; Richmond et al., 2001a; Sarmiento, 1985; 1998; Stern, 1975; Straus, 1949; Tuttle, 1967; 1969; 1974; 1975).

To explore the issue of knuckle walking in human evolution, much attention has been paid to the morphology of the metacarpals and wrists of hominins and extant

primates in attempt to isolate a "knuckle-walking signal" (Dainton and Macho, 1999; Inouye and Shea, 2004; Kivell and Schmitt, 2009; Matarazzo, 2008; Richmond and Strait, 2000; Richmond et al., 2001; Tuttle, 1967; 1969). This "signal" would be a morphological feature (particularly within the manus) that can be linked to knuckle walking to the exclusion of other locomotor patterns, specifically those hypothesized to be alternative ancestral conditions (quadrupedalism, suspension, or climbing). The presence or absence of a "knuckle-walking signal" in the distal radius and metacarpals has been hotly contested (Dainton, 2001; Inouye and Shea, 2004; Kivell and Schmitt, 2009). Richmond and Strait (2000) interpreted aspects of the morphology of the distal radius of African apes, *Australopithecus anamensis* and *A. afarensis* as evidence that bipedal hominins evolved from a knuckle-walking ancestor, while Dainton and Macho (1999), Dainton (2001), and Kivell and Schmitt (2009) defended the opposite view on the basis of other aspects of wrist morphology and developmental data. Williams's (2010) analysis of morphological integration of aspects of wrist and ray morphology supported Richmond and Strait's (2000) interpretation.

In addition to this search for a morphological feature, kinematic and behavioral studies of the extant hominoids have also been undertaken. These studies were designed to characterize the mechanics of knuckle walking and to determine whether knuckle walking differences exist between *Pan* and *Gorilla*. The studies have revealed one main difference between the African apes: chimpanzees are more variable in hand and arm position and digit use than gorillas. Tuttle (1967) observed that with chimpanzees, weight is primarily focused on digits 3 and 4, and the hands are placed at various angles to the

direction of movement during knuckle-walking bouts. In contrast, gorillas consistently contact the ground with all four digits 2-5 during knuckle-walking bouts (Tuttle 1969). In her study of ontogenetic changes in the kinematics of hand posture and digit use in African apes, Inouye (1994) observed no behavioral changes in digit use throughout ontogeny. She also confirmed Tuttle's (1967, 1969) earlier results and noted that chimpanzees and bonobos use digits 2 and 5 less frequently than gorillas, and gorillas consistently touch down on all four digits. Only recently has manual pressure data been used to examine the role of knuckle walking in hominin evolution (Wunderlich & Jungers, 2009). This study captured pressure distribution patterns of the hands of a single pair of knuckle-walking chimpanzees during two intervals of time, separated by several years. The authors found that at age 4-5 years, pressure was highest on digits 2-3 when the manus was placed in a "palm-in" position (palm facing the body in a parasagittal plane), and highest on digits 3 and 4 when the manus was placed in a "palm-back" position (palm facing posteriorly). At age 7, pressure was highest on digits 2-3 in the palm-back position. They also found that pressure was significantly greater on digit 2 when the hand was in the palm-in position. This pressure study was undertaken with 2 relatively young individuals and no comparison groups.

Given this rich history of research into knuckle walking, it is surprising that pressure applications of the manus had not been examined in great detail and that little attention was paid to the manual middle phalanges as these are precisely the elements that support the weight of knuckle-walking apes. The manual *proximal* phalanges have been shown to be affected by the biomechanical loads imposed during locomotion (Richmond,

1998, 2007). Richmond (1998) found that proximal phalangeal curvature changed throughout ontogeny based on a primate's changing locomotor pattern. Specifically those primates that were suspensory showed increased curvature values as use of suspension increased, and those who were quadrupedal, displayed increasingly flatter proximal phalanges as they aged and use of quadrupedalism increased. Finite element analysis has revealed that increased curvature of the proximal phalanges acts to mitigate the strains placed upon these elements during suspension (Richmond 1998, 2007). Taken alone, examinations of proximal phalangeal curvature can only determine whether a primate is suspensory or not. When these elements are examined in the African apes (who use suspension as well as knuckle walking), they fall in between the highly suspensory orangutans and quadrupedal primates (Jungers et al. 1997; Richmond 1998; Stern et al. 1995). Studies of the middle phalanges are limited. Matarazzo (2008) showed that the curvature signal for suspension is weak in the middle phalanges, but finer discrimination of locomotor patterns can be ascertained when one compares the curvature values of the middle to the proximal phalanges. This study examined only the corresponding proximal and middle phalanges of digit 3, and so its applicability to a scarce fossil record may be limited.

Chapter Overviews

The research presented in this dissertation explores the larger issue of knuckle walking in the hominin lineage by examining how extant African apes (*Pan* and *Gorilla*) knuckle walk, and by exploring the external and internal morphology of both the proximal and middle manual phalanges. The main goal of this research is to find a strong

knuckle-walking feature, or "signal", within the manus that could be easily applicable to limited and possibly fragmentary fossil material. This signal would help contribute to the knuckle-walking hominin debate by providing better insight into the locomotor repertoires of extinct hominins.

Chapter 2 examines how *Pan* and *Gorilla* apply pressure to their manual middle phalanges during knuckle walking. Very little research has been done on how pressure is applied to the primate manus. Prior to the research conducted here, there existed only one study of manual phalangeal pressure during knuckle walking (Wunderlich and Jungers, 2009), and one study of palmar pressure for the terrestrial quadrupedal primate, the Olive Baboon (Patel and Wunderlich, 2010). As described above, Wunderlich and Jungers' (2009) knuckle-walking pressure study involved only two relatively young individuals and offered no comparative sample of the only other extant knuckle-walking primate, the gorilla. Chapter 2 provides pressure data from a wider sample of adult and juvenile chimpanzees, and includes the first pressure data (manual or pedal) on gorillas. This inclusion of both gorillas and chimpanzees allows for an examination of potential differences within the two lineages of hominoids. In addition to exploring differences in pressure application, this chapter also quantifies variation in hand placement and preferred digit use by each individual. Kinematic studies have shown that gorillas are much more consistent in their use of a pronated arm posture than chimpanzees and contact the ground with digits 2-5 but how these differences affect the stress placed upon the phalanges has yet to be quantified.

Chapter 3 is a continuation of the research on phalangeal curvature that began with my 2008 study of the manual phalanges of the third digit. My 2008 study showed that one can construct a ratio between middle and proximal phalangeal curvature (which I called the "Index of Relative Curvature") that allows for finer discrimination between locomotor categories than is seen if just comparing the proximal phalangeal curvature values alone. Increased proximal phalangeal curvature can indicate suspension, while flatter, may indicate less suspension or possibly quadrupedalism. In contrast, the Index of Relative Curvature differentiates among knuckle walkers (*Pan troglodytes* and *Gorilla gorilla*), quadrupeds (*Macaca* spp. and *Sapajus apella*), brachiators (*Hylobates lar*) and quadrumanus climbers (*Pongo pygmaeus*). If we are to use this index in paleoanthropological research, it must be shown to be useful when derived from digits 2, 3, 4, or 5. This is because the fossil record is sparse, and it isn't often that both middle and proximal phalanges are recovered from a single digit, let alone, specifically, the third digit. Here I ask whether the Index of Relative Curvature provides a strong signal: 1) when measured on digits 2-5, 2) when indices are composed of elements from different digits within the same manus, and 3) when they are composed of elements from different individuals of the same species. If the signal is as strong when indices are composed from different elements within the same hand, or from different individuals it would be a much more useful tool for the study of limited fossil phalangeal material.

Chapter 4 builds upon this search for a morphological signal that can be used by paleoanthropologists to identify knuckle walking in fossils by exploring the internal structure of the digits. MicroCT scanning has provided a non-destructive way to examine

trabecular bone in fine detail, so it is an attractive tool to examine rare manual elements of extant and extinct animals. Trabecular bone has been shown to align along an axis of primary function (Barak et. al., 2011; Fox and Keaveny, 2001; Jacobs, 2000; Keaveny et. al., 2001; Mittra et. al. 2005; Polk et. al., 2008; Pontzer et. al, 2006). Within primates, the femoral and humeral head trabecular structure has been examined in a number of taxa and locomotor differences within these elements have been observed (DeSilva and Devlin, 2012; MacLatchy and Muller, 2002; Ryan and Ketchum, 2002; Ryan and Shaw, 2012; Ryan and Walker, 2010; Shaw and Ryan, 2012). This chapter examines the trabecular bone structure of the manual phalanges and metacarpals of a subset of the individuals included in the curvature analysis to determine whether an internal biomechanical signal is present within these elements. Building on the external morphology findings (curvature differences), we can predict internal structural difference across locomotor groups and within a single digit, particularly with knucklewalkers who have "flattened" middle phalanges coupled with curved proximal phalanges. The flattened middle phalanges experience compression during knuckle walking, but both proximal and middle phalanges experience tensile forces during suspension. A suite of trabecular bone features are explored in five locations on the third manual ray: the proximal and distal ends of the proximal and middle phalanges and the metacarpal head. Trabecular bone alignment differences located in particular anatomical zones would greatly add to the ability to discern locomotor patterns in fragmentary fossil elements for which the external structure cannot be reconstructed.

The final chapter summarizes the results of the pressure, phalangeal curvature and trabecular bone studies and interprets them in the broader context of the ancestral knuckle-walking hominin hypothesis. Differences in pressure application between two knuckle-walking taxa not only act to clarify differences seen in the morphology of the manus, but can be explored to elucidate issues of homology or homoplasy of knuckle walking, within African apes. Although there is no outgroup comparison for this analysis, as both *Homo* and *Pongo* practice widely different methods of locomotion thus making manual pressure comparisons impossible, we can still broadly explore the overall pattern of knuckle walking within the great apes and determine whether similarities or glaring differences can inform us of the possibility of convergence within the lineages. This chapter details how the pressure distribution data relates to the curvature differences noted across the manus of individual knuckle walkers, and how the patterns of curvature relate to what we see in the trabecular structure. We also see how differential pressure application within middle phalanges accounts for differences in proximal and distal trabecular bone alignment in these elements. Is there a definitive knuckle-walking signal within the structure of the manual elements? What inferences can we make about fossil hominins from these locomotor signals that may provide greater insight into the origins of bipedalism? These questions and others are explored in the final chapter.

CHAPTER 2

MANUAL PRESSURE DISTRIBUTION PATTERNS IN THE AFRICAN APES (*PAN* AND *GORILLA*)

Abstract

To understand the role of knuckle walking in hominin evolution, we need to better understand behavioral variation in knuckle walking, and specifically whether behavioral similarities between chimpanzees and gorillas are likely homologous. Differences in how the hands of gorillas and chimpanzees contact the ground while knuckle walking have been noted but not quantified: it is widely believed that gorillas maintain a pronated arm and contact the ground with digits 2-5 consistently, while chimpanzees have variable arm position and digit contact. Distribution of pressure across the manus, peak digital pressures, and hand position were quantified to further test these generalizations. Chimpanzees and gorillas make initial ground contact with the ulnar aspect of the hand, and pressure then moves radially. They differ in which digit usually makes final contact and receives maximum pressure, and in hand position during contact. Gorillas regularly use a palm-back hand position and touch-off with digit 2. They show less variation in pressure application across the digits. Chimpanzees are more variable in hand position and pressure application. These differences may relate to aspects of locomotor behavior that are unrelated to knuckle walking; chimpanzees are more suspensory than gorillas. Nevertheless there are some commonalities that appear to be synapomorphic, and that would in any case require explanation if they do not signal knuckle walking in the common ancestor of chimpanzees and gorillas (and by implication, humans). In both, hand position plays a key role in determining which digit acts as the final touch-off element.

Introduction

Previous studies addressing the role knuckle walking played in human evolution have focused primarily on morphological analyses of the wrists, metacarpals, and to a lesser extent the phalanges of extant primates and fossil hominins (Dainton and Macho, 1999; Inouye and Shea, 2004; Kivell and Schmitt, 2009; Matarazzo, 2008; Richmond and Strait, 2000; Richmond et al., 2001; Tuttle, 1967; 1969). The presence or absence of a "knuckle-walking signal" in the wrist and metacarpals has been hotly contested (Dainton, 2001; Inouye and Shea, 2004; Kivell and Schmitt, 2009). Richmond and Strait (2000) interpreted aspects of the morphology of the distal radius of African apes, *Australopithecus anamensis* and *A. afarensis* as evidence that bipedal hominins evolved from a knuckle-walking ancestor, while Dainton and Macho (1999), Dainton (2001), and Kivell and Schmitt (2009) defended the opposite view on the basis of other aspects of wrist morphology and developmental data. Williams's (2010) analysis of morphological integration of aspects of wrist and ray morphology supported Richmond and Strait's (2000) interpretation.

Little research has focused on the morphology of the middle phalanges in knuckle walkers, despite the fact that it is precisely these skeletal elements that should be affected most directly by knuckle walking. Curvature of the manual proximal phalanges of primates varies with levels of suspension (Jungers et al, 1997; 2002; Richmond, 1998). The middle phalanges of knuckle walkers are the primary load bearers during knuckle walking bouts. Therefore one could predict that these elements should be relatively

straighter than the proximal phalanges (Richmond et al., 2001). This would allow for greater digit-to-surface contact area and increased dissipation of the compressive forces generated during knuckle walking. Examining the third ray, Matarazzo (2008) showed that chimpanzees and gorillas do in fact share relatively low middle phalanx curvature – a trait that distinguishes these species from orangutans. However, other aspects of manual morphology of chimpanzees and gorillas show strong differences. Gorillas have relatively shorter metacarpals and proximal phalanges and less inter-ray length variation than chimpanzees (Inouye, 1992). New data (Matarazzo, in prep.) on middle phalanx curvature for digits 2, 4, and 5 (as well as 3) show that, whereas chimpanzees and gorillas share the same pattern of variation in middle phalanx curvature across the manus, with greatest flattening in rays 3 and 4, chimpanzees have greater dispersion around their mean (with a coefficient of variation of 11.8 cf. 10.4 in gorillas), and higher curvature values for digit 5. Lower variation in middle phalanx length and curvature in gorillas may relate to lower variation in pressure distribution during knuckle walking, a phenomenon that can be elucidated by studying how pressure is applied to the middle phalanges.

Pressure distribution analysis has gained popularity within the anthropological literature as a means to quantify footfall patterns in a variety of primate taxa. Most of this research focuses on plantar pressure as its relates to the origin of bipedalism in the hominin lineage (Barden et al., 2010; Berillon et al., 2010; Bertsch et al., 2004; D'Aout et al., 2004; Vereecke et al., 2003; Vereecke et al., 2005; Vereecke & Aerts, 2008; Wunderlich, 1999). Only recently has manual pressure data been used to examine the

role of knuckle walking in hominin evolution (Wunderlich & Jungers, 2009). Much of the prior data on hand use in knuckle walking were behavioral observations. Tuttle (1967) observed that chimpanzees concentrated weight on digits 3 and 4 and placed their hands at various angles to the direction of movement during knuckle-walking bouts. Inouye (1994) studied ontogenetic changes in the kinematics of hand posture and digit use in gorillas, chimpanzees, and bonobos. She observed no behavioral changes in digit use throughout ontogeny; chimpanzees and bonobos use digits 2 and 5 less frequently than gorillas, and gorillas consistently touch down on all four digits.

Patel and Wunderlich (2010) examined the palmar pressure distribution as measured in two adult olive baboons at different walking speeds. They demonstrated that, as speed increases, palmar contact increases. They hypothesized that greater palmar contact might mitigate the increased strain that may be placed on the metacarpals at higher speeds. Knuckle walkers transmit force through the digits only so palmar contact cannot be used to mitigate strain.

Only one study of pressure variation describes the manus of knuckle walkers (Wunderlich and Jungers, 2009). This study captured pressure signals of the manus of a single pair of knuckle-walking chimpanzees during two intervals of time, separated by several years. The authors found that at age 4-5 years, pressure was highest on digits 2-3 when the manus was placed in a "palm-in" position (palm facing the body in a parasagittal plane), and highest on digits 3 and 4 when the manus was placed in a "palm-back" position (palm facing posteriorly). At age 7, pressure was highest on digits 2-3 in

the palm-back position. They also found that pressure was significantly greater on digit 2 when the hand was in the palm-in position.

To determine whether proto-hominins were knuckle walkers, it is vital that the biomechanics of knuckle walking, the forces being applied to the rays, and the resulting skeletal correlates be better understood. This paper examines manual pressure patterns of extant knuckle walkers (chimpanzees and gorillas). I have two main goals; the first is to verify the generality of prior observations. Is it true that gorillas distribute pressure more evenly across all digits than do chimpanzees? Can differences in pressure be related to differences in manual morphology? Are changes in hand position correlated with how pressure is applied? If Wunderlich and Jungers' (2009) observations hold for a broader sample of chimpanzees, pressure should be higher on digit 2 in the palm-in position than in the palm-back position. The second goal is to determine whether there are common aspects in the execution of knuckle walking that distinguish knuckle walkers from other animals. Was knuckle walking independently derived in the chimpanzee and gorilla lineages, or was some form of knuckle walking shared by their common ancestor (and by implication, the common ancestor of chimpanzees, gorillas, and humans)? If the latter, can that form of knuckle walking be characterized?

Methods

This study included six adult (18 year-old, 1 male, 5 females) and two juvenile (3 year-old, 1 male, 1 female) *Pan troglodytes*. These chimpanzees were part of the Cognitive Evolution Group (University of Louisiana at Lafayette) and were trained to

perform in tasks related to cognition studies. They were fully habituated to human presence, trained to self-transfer from their housing to testing unit, perform in cognitive testing on a regular basis, and worked with the same trainers for several years. The chimpanzees had access to outside, open-air enclosures and arboreal supports in testing and housing units. They were housed together in one area and individuals or pairs of chimpanzees were separated from the communal group to a cognitive testing room (11' x 8' x 7') where the pressure mat was secured to concrete flooring. Individuals participated in a daily "trial" that lasted no more than 30 minutes each for 11 days. The pressure mat was set flush within a larger frame (4' x 31" x 1") and covered with a non-slip vinyl to prevent the chimpanzees from targeting the equipment during a pass. The frame was placed in front of a path the chimpanzees regularly used to reach a "marker" situated on a wall. As the chimpanzees entered, they crossed the mat to touch their marker. They repeated this movement several times in a given trial. The chimpanzees were given food rewards at the end of each trial.

The gorilla groups were housed at two separate zoo facilities: the Lincoln Park Zoo, Chicago, IL (LPZ) and the Franklin Park Zoo, Boston, MA (FPZ). The LPZ group consisted of a silverback (19 years old), one male infant (2 years old), and two adult females (18 and 12 years old). The FPZ group consisted of two silverbacks (both 18 years old), two adult females (39 and 30 years old) and one infant female (weight ~5lbs) carried continually by her mother Kiki. Both gorilla groups were habituated to the presence of their keepers, but not to performing specific tasks. At both zoos, the pressure mat was placed in an off-exhibit corridor with concrete flooring. The corridors were

sufficiently long to ensure a full pass across the mat, but sufficiently short to prevent fast running. Data were collected opportunistically when the gorillas entered and exited the off-exhibit housing twice daily. At the FPZ, the frame encasing the mat filled the entire corridor from the off-exhibit housing to the main exhibit area (56" x 34" x 1"). At the LPZ, the frame (6' x 38" x 1") was set within a long transfer chute (33' x 40" x 40"). The chute consisted of a ceiling and one wall made of reinforced steel caging, one wall of concrete blocks and a concrete floor. At both zoos, the frame was covered in non-slip vinyl to disguise the location of the pressure mat, and the mat was set off-center within the frame to better capture a hand print. Gorillas at both institutions had access to arboreal supports and softer (non-concrete) flooring in exhibit housing. Due to differences in enclosure structures and training, chimpanzees made contact with the pressure mat more frequently than did gorillas (Table 2.1).

Pressure distribution data were collected using an RS Scan footscan pressure mat (0.5 x 0.4 x 0.008 m; 4096 sensors; 150 Hz Max. Freq.) and RS Scan footscan software. Individual digital pressure for rays 2-5, center of pressure movement across the hand, location of peak pressure (N/cm^2) on the manus for each step, bout time (in milliseconds), initial contact digit (2-5), and "touch-off" digit (2-5) were determined for each recorded pressure imprint (Figure 2.1). Bout time was used to assess speed of each knuckle-walking step and was calculated from the time the initial contact was made to the final touch-off point. The initial contact digit is the digit that makes first contact with the ground. The "touch-off" digit is defined as the digit that is used to push off to the subsequent step. It is the last digit in contact with the pressure mat as the hand lifts up to

a subsequent step. Only complete contact "steps" in which the entire hand had the ability to contact the pressure mat during a walking bout were scored and analyzed. Steps in which an animal was reversing or stopping were excluded from analysis. The RS Scan software is designed for a human foot, thus knuckle walking prints are originally color-coded to represent the foot segments (i.e. forefoot, heel, metatarsals, digits). In this manner, a single digit may be subdivided into heel, mid foot, etc. Knuckle-walking prints were manually color coded to accurately represent digits; individual digits were each given their own color code so resulting pressure outputs were correctly representing a middle phalanx print. These color coded prints are "scored contacts" (Table 2.1). To measure touch-off digit preference, digits were assigned numerical values corresponding to their ray number, and these values were averaged for specified groups. A mean of 2.5 signals equal preference for digits 2 and 3. A mean of 2.8 indicates greater preference for digit 3 or other, more ulnarly placed, digits. This is not a measure of the movement of the center of pressure.

All statistical analyses were conducted using SPSS version 20. Before considering similarities and differences between chimpanzees and gorillas, the influence on manual pressure of confounding variables such as body mass (in kiligrams), sex, age (juveniles vs. adults), and walking speed (which is inversely correlated with bout time) was tested using correlation and multiple regression analysis. A Discriminant Function Analysis was used to capture the primary differences in hand use between gorillas and chimpanzees; it examined peak pressure on digits 2-5, hand position, touch-off digit, touch-off pressure, initial contact digit, initial contact pressure, and digit with the highest

pressure per step. ANOVAs with Tukey's test of Honestly Significant Differences (HSD) were used to assess differences in the amount of pressure applied to the touch-off digit within and between taxa, and to assess differences in bout time. Pearson's correlation coefficients were used to examine the relationships between touch-off or initial contact digit and the digit with the highest pressure per step. Chi-square analyses were conducted to assess differences in placement of peak pressure in the palm-back and palm-in positions, frequency of use of palm-back and palm-in hand positions, and preferred touch-off digit both within and between taxa. Fisher's exact tests were used to assess differences between chimpanzees and gorillas in peak pressure distribution across the manus. Paired t-tests were used to examine pairwise differences in peak pressure values between digits.

Skeletal elements were also measured to assess morphological differences within and across taxa. Total length measurements (mm) of the metacarpals and proximal phalanges of digits 2-5 were taken from specimens housed at the American Museum of Natural History, New York, NY; Cleveland Natural History Museum, Cleveland, OH; Field Museum, Chicago, IL; Museum of Comparative Zoology, Cambridge, MA; and National Museum of Natural History, Washington DC. Samples included 87 adult gorillas (*Gorilla gorilla*: 59 males and 28 females) and 53 adult chimpanzees (*Pan troglodytes*: 35 males and 18 females). The length of the metacarpal plus proximal phalanx for each ray (2-5) was measured and then compared across the manus for each species using ANOVA with Tukey's HSD to assess the structure of the knuckle-walking "platform" for the load-supporting middle phalanges.

Results

The Influence of Body Size, Sex, Walking Speed, and Age on Touch-off Pressure and Peak Pressures for Digits 2-5

Touch-off pressure and average peak pressure values (digits 2-5) for each individual are displayed in Table 2.2. When we consider the effect of body mass on touch-off pressure, there is a negative relationship (smaller individuals have increased peak pressures on their digits). This relationship is seen when we consider chimpanzees and gorillas together in a pooled sample and when they are examined separately. Although the correlation for adult chimpanzees is not significant, it still reflects a negative relationship.

A significant correlation between body mass and touch-off pressure is seen when adult chimpanzees and adult gorillas are pooled ($r = -0.203$, $N = 146$, $P = 0.014$). However, this is a negative correlation, indicating that pressure per unit area is actually greater in the lighter individuals. The influence of body mass on touch-off pressure remains negative when other potentially explanatory variables are added to the mix. A multiple regression of touch-off pressure on body mass, bout time and sex in adult chimpanzees and gorillas pooled reveals little influence of any of these potentially confounding variables. The total variance explained (R^2) is low (0.09), and only body mass is significant ($t = -2.85$, $P = 0.005$).

Similar results hold when digits are considered independently and peak pressure is evaluated for each. The total variance explained averages 0.13 and never exceeds 0.18. None of our explanatory variables contributes significantly to explaining variation in peak pressure for digit 2. Body mass is significant for digits 3-5, but the t value is negative in each case. Sex is significant for digits 3 and 5, with males showing higher peak pressures per unit area than females, but this relationship does not hold for digit 4. Bout time is insignificant except for digit 5 ($P = 0.02$), with slower speed (longer bout time) correlated with higher pressure values.

When chimpanzees and gorillas are considered separately, the negative relationship between touch-off pressure and body mass holds. For adult chimpanzees, none of our explanatory variables explains touch-off pressure ($R^2 = 0.05$). Body mass and touch-off pressure are not significantly correlated in adult chimpanzees ($r = 0.095$, $N = 110$, $P = 0.33$) or adult gorillas ($r = -0.256$, $N = 38$, $P = 0.13$). Body mass does not explain peak pressure for any single digit, and neither does bout time. Sex is significant for digits 3 and 5, but the direction of the significance is reversed, with females showing greater peak pressures on digit 5, and the reverse for digit 3. However, once again, the total variance explained is low for all relationships, even when some of the variables explain significant portions of that variance ($R^2 = 0.11$ for digit 3 and 0.23 for digit 5).

For adult gorillas, body mass has a significant ($P = 0.01$) but negative relationship with touch-off pressure. None of the other explanatory variables is significant. Body mass explains peak pressure for only two digits (in this case, digits 3 and 4), but the

relationship is negative. Bout time has no impact on peak pressure for any single digit. Sex is significant for digit 4 only, with males showing higher peak values than females.

Given the rarity of juveniles in our gorilla samples, the effects of age can be tested only on chimpanzees. T-tests comparing juvenile and adult chimpanzees show significant differences in touch-off pressure ($t = 9.61$, $df = 154$, $P < 0.001$) and peak pressures on all digits with the exception of digit 5 (with adults experiencing higher pressures in digits 2 through 4). The t-values for digits 2 through 4 range from 6.64 to 9.11, which, with 154 degrees of freedom, yield P values < 0.001 in all cases. In juveniles, initial contact is made with the ulnar aspect of the hand and the center of pressure moves radially, as in adults, but then rolls back towards the ulnar aspect of the hand. This pattern gives juveniles an unstable, "wobbly" appearance as they knuckle walk, causing increased pressure on digit 5.

Chi Square analyses show that adult chimpanzees differ from juveniles for hand position ($X^2 = 8.8$, $df = 1$, $P = 0.003$): juveniles use the palm-back position more than expected (68% of steps) while adults use palm-in more than expected (58% of steps). Touch-off digit is also significantly different between adults and juveniles ($X^2 = 15.63$, $df= 2$, $P < 0.001$). Juveniles touch-off with digit 3 89.4% of the time while adults show less preference for digit 3, using digit 2 37% of the time and digit 3 57% of the time.

Behavioral Similarities between Gorillas and Chimpanzees

All knuckle walkers contact the ground with the ulnar aspect of the hand and then the center of pressure moves radially. Among gorillas, the fifth digit is universally the initial contact digit; in contrast, chimpanzees sometimes curl digit 5 under and contact the ground initially with digit 4 (19.7% of all steps). The position of the hand (palm-back or palm-in) affects whether digit 2, 3, or 4 is used for touch-off in adults. Hand position affects the placement of the digits, which in turn affects which digit is used for touch-off. The main differences between taxa are thus brought about by differences in digit length, which affects digit placement differently (depending on hand position) in the two taxa. Gorillas display less variability than chimpanzees; in effect, their manual behaviors can be viewed as a subset of those seen in chimpanzees. For each species, the touch-off digit is significantly correlated with the digit with the highest pressure per step (for chimpanzees, $r = 0.41$, $N = 156$, $P < 0.001$; for gorillas, $r = 0.38$, $N = 38$, $P = 0.02$). For each species, also, the act of pushing off to the next step places considerable pressure on the digits and that pressure is consistently significantly greater than that of the initial ground contact digit, as shown using paired t tests. (For adult chimpanzees, touch-off mean pressure = 2.84N/cm^2 SD =1.2, initial contact mean pressure = 1.38N/cm^2, SD = 0.99, $t = 11.62$, $df = 109$, $P < 0.001$. For adult gorillas, touch-off mean pressure = 2.25 N/cm^2, SD = 1.4, initial contact mean pressure = 1.46N/cm^2, SD = 0.90, $t = 3.72$, $df = 35$, $P = 0.001$.) There is also no correlation in either species between the initial contact digit and the digit with the highest pressure (for chimpanzees, $r = 0.02$, $N = 110$, $P = 0.87$; for gorillas, $r = 0.09$, $N = 36$, $P = 0.59$.)

Behavioral Differences between Gorillas and Chimpanzees

Chimpanzees and gorillas differ in several important ways. A discriminant function analysis of adults only was successful at differentiating chimpanzees from gorillas. Function 1 has a strong canonical correlation of 0.57, and is highly significant ($X^2 = 78.35$, df = 10, $P < 0.001$). Gorillas differ from chimpanzees in their consistent use of the palm-back hand position and greater use of digit 2 in touch-off. In contrast, chimpanzees use both hand positions regularly and touch-off with greater frequency on digits 3 and 4. This analysis was successful in classifying individuals as either gorillas or chimpanzees with 88.9% accuracy (87.9% of cross-validated grouped cases correctly classified).

Chimpanzees exhibit considerably more individual variation than do gorillas. Chi-square analyses of adult chimpanzees reveal significant individual differences in touch-off digit preference ($X^2 = 30.68$, df = 10, P =0.001) and favored hand position (palm-in or palm-back; $X^2 = 10.82$, df = 5, P = 0.05). Individual chimpanzees use both hand positions in different proportions. Individual adult gorillas show no significant differences in favored hand position or touch-off digit. All gorillas used palm-back hand positions more than expected (100% for 5 individuals, 60% and 75% for the remaining two) and touched-off with either digit 2 or 3.

Touch-off pressure and touch-off digit are significantly correlated in both chimpanzees ($r = -0.319$, N = 110, $P < 0.001$), and gorillas ($r = 0.367$, N = 36, P = 0.028).

However, the chimpanzee correlation is negative revealing a shift in touch-off location towards the radial aspect of the hand as pressure increases. Gorillas have a positive correlation; touch-off location shifts ulnarly as pressure increases. Gorillas have a touch-off digit mean of 2.37. The center of pressure moves radially in a given step and touch-off occurs more frequently on digit 2. The mean for chimpanzees (2.77) signals an average closer to digit 3. These means are significantly different ($t = 3.41$, $df = 144$, $P = 0.001$).

As stated above, chimpanzees and gorillas differ significantly in their use of hand position ($X^2 = 16.93$, $df = 1$, $P < 0.001$). Chimpanzees use both hand positions at approximately equal rates: palm-back (42% of steps) and palm-in (58% of steps). Gorillas favor palm-back (86%), and only 5 out of 36 steps were palm-in (14%). Touch-off digit also differs significantly between the taxa ($X^2 = 10.76$, $df = 2$, $P = 0.005$). Chimpanzees touch-off frequently on digits 2, 3, and 4. Gorillas use digits 2 and 3 only, with most steps touching off on digit 2 (67%).

When hand position is taken into account, preferred touch-off digit also differs between the species ($X^2 = 42.92$, $df = 2$, $P < 0.001$). In the palm-back position, touch-off occurs 86% of the time on digit 3 for chimpanzees. In gorillas, it occurs mainly on digits 2 (61% of steps), and 3 (39% of steps). When chimpanzees knuckle walk using the palm-back position, digit 3 is regularly positioned in front of the other rays making it the final contact element (Figure 2.2). Gorillas show a greater alignment of the digits in the palm-back position shifting touch-off either to digit 2 or 3 (Figures 2.3 and 2.4). In the palm-in

position, there is no significant difference in touch-off digit between species; both favor digit 2, although gorillas do so more consistently than chimpanzees.

Fisher's exact tests comparing the distribution of touch-off digit "counts" (how many times either digit 2, 3, 4, or 5 was used as a touch-off digit) showed no significant differences between taxa when both palm-in and palm-back steps were included ($P = 0.71$) or when only palm-in contacts were compared ($P = 0.40$). However, highly significant differences were seen in the palm-back hand position ($P < 0.001$).

Hand position also affects the amount of pressure applied to digits in chimpanzees but not gorillas. In the palm-in hand position, significantly greater pressure is applied to digits 2 and 5 than in the palm-back position for chimpanzees (digit 2: $t = 3.9$, $df = 107$, $P < 0.001$; digit 5 $t = 2.99$, $df = 108$, $P = 0.003$). Digit 3 is not significantly different but greater pressure is seen in the palm-in position ($t = 1.74$, $df = 108$, $P = 0.08$). Digit 4 received significantly greater pressure in the palm-back position (digit 4 $t = -1.9$, $df = 74$, $P = 0.05$). No significant differences in pressure application to the digits were seen in gorillas in the palm-back versus palm-in hand positions. However, this result could be affected by the lower frequency of palm-in steps used by this taxon.

T-tests comparing pairwise differences between the maximum pressures (N/cm^2) for digits 2-5 for each walking bout were conducted for adult chimpanzees and gorillas. Within chimpanzees, only pairings with digit 5 show a significant difference. Digit 5 receives significantly less pressure than digit 2 ($t = 8.58$, $df = 109$, $P < 0.001$), digit 3 ($t =$

11.96, df = 109, P <0.001), and digit 4 (t = 9.69, df = 109, P <0.001). The amount of pressure placed on digits 2, 3, and 4 is not significantly different for this species when individuals are pooled. For gorillas, only pressure values for digits 2 and 4 do not differ significantly in the pooled adult samples. Digit 3 is significantly greater than digit 2 (t = -2.05, df = 35, P = 0.048), digit 4 (t = 3.2, df = 34, P = 0.003), and digit 5 (t = 5.22, df = 31, P < 0.001). Digit 5 is significantly lower than digit 2 (t = 3.51, df = 31, P = 0.005), and digit 4 (t = 3.3, df = 31, P = 0.002). When paired t-tests are run for individual chimpanzees and gorillas, results are quite different for the gorillas. Only one gorilla shows significant differences in pressure application across her digits (Table 2.3); the others distribute pressure evenly across digits 2-5.

Manual morphology in gorillas and chimpanzees.

Chimpanzees and gorillas possess different digit length patterns within the manus. ANOVA tests showed significant differences between the metacarpal plus proximal phalanx lengths of digits 2-5 within chimpanzees (F = 83.61, df = 3, P <0.001) and gorillas (F = 34.22, df = 2, P < 0.001). In chimpanzees, only digits 2 and 4 do not differ significantly in length (mean difference = 4.29 mm, SE = 2.05, P = 0.136). Digit 3 is significantly longer than digit 2 (mean difference = 6.96 mm, SE = 2.05, P < 0.005), digit 4 (mean difference = 11.17, SE = 2.07, P < 0.001) and digit 5 (mean difference = 30.87, SE = 2.07, P <0.001), and digit 5 is significantly shorter than 2 (mean difference = -23.99, SE = 2.05, P < 0.005), 3 (mean difference = -30.87, P < 0.001), and 4 (mean difference = -19.69, SE = 2.06, P < 0.001). For gorillas, digit 5 is significantly shorter than digit 2 (mean difference = -16.2, SE = 2.2, P < 0.001), digit 3 (mean difference = -

21.35, SE = 2.2, P < 0.001), and digit 4 (mean difference = -13.31, SE = 2.2, P < 0.001). Digits 2, 3 and 4 are not significantly different from each other. The same pattern is seen when males and females of each species are considered separately (Figure 2.5). Digit 3 is significantly longer than digits 2, 4 and 5, and digit 5 is significantly shorter than digits 2, 3 and 4 in both female and male chimpanzees. Male and female gorillas each have no significant variation between digits 2-4, and digit 5 is significantly shorter.

Male gorillas have significantly longer digits than female gorillas (t ranges from 7.49 to 13.4, df = 84, P <0.001) and male chimpanzees (t ranges from 6.02 to 7.78, df = 91, P < 0.001). Chimpanzees do not show significant differences between the sexes for any digit. Significant differences are seen between the digit lengths of female chimpanzees and gorillas: female chimpanzees have significantly longer digits 2 (t = 2.7, df = 43, P = 0.008) and 3 (t = 3.83, df = 43, P < 0.001). No significant differences were seen in digits 4 or 5 for the females.

Discussion

Previous research has described differences in the knuckle-walking patterns of chimpanzees and gorillas: the latter are more consistent in their use of a fully pronated arm and make contact with all four digits 2-5 when knuckle walking. One of the main goals of this paper was to expand the quantitative database for chimpanzees and to quantify manual pressure for the first time in gorillas. A second goal of this research was to contextualize differences between gorilla and chimpanzee patterns of knuckle walking in light of the question of knuckle-walking origins. Most of the observations reported

here are consistent with earlier accounts of dynamic pressure patterns in chimpanzees (Wunderlich and Jungers 2009) and with observational and kinematic accounts of chimpanzees and gorillas (Inouye 1994; Tuttle 1967). Chimpanzees do indeed display greater variation than gorillas in their touch-off digit preference and in hand position. However, this paper also shows that hand position is a major factor influencing touch-off and maximum pressure in both chimpanzees and gorillas. In the palm-back position, chimpanzees touch off mainly with digit 3, because of the position of digit 3 with the palm facing backwards. In the palm-in position, digit 2 is most forward and touch-off occurs more frequently on digit 2. Gorillas differ from chimpanzees because their digits are more evenly aligned. Gorillas show no differences in pressure application based on hand position and show more even distribution of pressure across the manus in any given step. Both taxa place significantly less pressure on digit 5 than the other elements.

Inouye (1994) showed that gorillas have relatively shorter metacarpals and less variable phalangeal lengths than chimpanzees. Skeletal data presented here confirm these observations. This difference between gorillas and chimpanzees in manual morphology and the knuckle-walking platform affects which digit is placed farthest forward in a given hand position. It therefore affects which digit is most likely to receive maximum pressure and thus serve as touch-off digit. Given the forward placement of digit 3 in chimpanzees when the manus is in the palm-back position, the shift in function of digit 3 in these animals is unsurprising. A similar shift does not occur in gorillas, precisely because of the more even alignment of the digits.

More research is needed to determine the adaptive value to chimpanzees of digit length variability. Although both species travel terrestrially via knuckle walking, chimpanzees spend more time in suspensory postures than gorillas (Doran 1993; 1997; Inouye 1994; Tuttle 1967). The more even ray lengths within the manus of gorillas may create a more stable, even platform across which the heavier gorillas can distribute their weight when knuckle walking. While it is unclear if the variation in digit lengths of chimpanzees is functionally adaptive to suspension, it is has been shown that the relatively longer manual digits of chimpanzees are biomechanically more efficient for an enhanced grip during climbing and suspension (Cartmill, 1985; Susman, 1979). Chimpanzee and gorilla pressure pattern differences while knuckle walking may thus reflect differences in manual morphology, in turn related to variation in positional behavior – i.e., the relative amount of time spent climbing, in forelimb suspension or knuckle walking.
They may therefore provide little support for a convergent origin of knuckle walking.

To be sure, this research documents behavioral differences that can be marshaled in support of convergence. However, the pattern of manual pressure distribution observed when gorillas knuckle walk also occurs in chimpanzees; gorillas exhibit, in effect, a subset of the individual variability of chimpanzees. Chimpanzees use the palm-back hand position preferred by gorillas in approximately half the walking bouts recorded. They also, like gorillas, use either digit 2 or 3 as the final contact for the step in this hand position. The main factor affecting touch-off digit for both species is the placement of the individual rays in each hand position. Touch off is most likely to occur on those digits that are farthest forward in the direction of movement. To be certain, there are

some morphological features of the gorilla manus that do not characterize chimpanzees, specifically the relatively shorter metacarpals and phalanges and decreased variability in digit length across the manus. These differences do not preclude knuckle walking from being ancestral for gorillas and chimpanzees (and by implication, humans). Extant gorillas have a hand morphology that reflects their greater reliance on knuckle walking. The greater variation in both manual morphology and knuckle-walking patterns of chimpanzees may reflect an ancestral condition of greater suspension coupled with limited terrestrial knuckle walking.

Conclusions

Chimpanzees use a great variety of hand positions during knuckle walking which affects how pressure is distributed and which digit receives maximum pressure. In contrast, gorillas are less variable in their hand placement. They use a palm-back hand orientation and use digits 2 and 3 as the touch-off digit. Hand position is an important factor influencing which digit propels the hand into the subsequent step. Thus, the touch-off digit is significantly correlated with the digit that has maximum pressure in a given walking bout. The variability of hand orientation of chimpanzees alters which digit is the touch-off and which receives maximum pressure. Chimpanzees touch-off frequently using digit 3 in the palm-back position; however pressure shifts radially and is highest on 2 or 3 in the palm-in position. Gorillas show less variation in pressure application across the digits and spread weight more evenly across the manus.

The similarities of chimpanzees and gorillas support a common origin for knuckle walking. The primary difference between the two (i.e., chimpanzees' greater reliance on digit 3 in the palm-back position) can be related to morphological differences in the structure of the hand. Chimpanzees have greater variation in digit length within their hands, while gorillas have relatively shorter rays and less length variation. Proportionally longer digits with greater length variation provides for an "uneven" platform for weight distribution during knuckle walking. The more even platform for weight distribution in gorillas may have evolved with their decreased reliance on forelimb suspension and climbing, coupled with an increased reliance on terrestrial knuckle walking.

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Table 2.1: Highest digit pressure values for each scored contact step.

Genus	**Sex/Age (yrs)/ Weight (kg)**	**Name**	**Scored Contacts**	**Number of times digit experienced peak pressure for scored contacts**			
				II	**III**	**IV**	**V**
Pan	M/ 18/ 68	Apollo	18	4	9	4	1
	F/ 18/ 54	Mindy	10		6	4	
	F/ 18/ 59	Jadine	11	3	4	3	1
	F/ 18/ 49	Candy	10	4	1	3	2
	F/ 18/ 43	Brandy	25	10	1	14	
	F/ 18/ 75	Kira	36	17	11	8	
	F/ 3/ 9.5	Manetta*	15	6	4	3	2
	M/ 3/ 12	Zack*	31	2	7	9	13
Gorilla	M/19/195	Kwan	5	2	1	2	
	F/ 18/63	Bulera	5	3	1	1	
	F/ 12/54	Madini	12	2	7	3	
	M/ 2/18	Amare*	2	2			
	M/ 18/168	Okie	4	2		1	1
	M/ 18/184	Little Joe	2	1		1	
	F/ 39/111	Gigi	6	3	1	1	1
	F/ 30/103	Kiki	2	2			

*juvenile

Table 2.2: Average pressure (N/cm^2) placed on digits 2-5.

Genus	Individual	Digit 2	Digit 3	Digit 4	Digit 5	Touch-off Pressure
Pan	Kira	3.15	2.42	2.41	1.1	3.18
	Brandy	2.64	2.4	2.94	0.62	3.09
	Mindy	**	2.33	2.16	1.25	2.46
	Jadine	1.61	1.69	1.52	0.87	1.76
	Candy	2.64	2.39	2.03	1.49	2.63
	Apollo	2.51	3.06	2.34	1.94	3.0
	Manetta*	0.79	1.05	0.98	0.3	1.21
	Zack*	0.65	1.16	1.49	1.28	1.13
Gorilla	Bulera	2.36	2.92	2.16	1.48	3.38
	Medini	1.65	2.63	1.93	0.93	2.41
	Kwan	1.98	2.16	1.12	0.86	2.2
	Gigi	1.1	2.17	1.07	0.87	2.18
	Okie	1.45	1.4	1.63	1.13	1.6
	Joe	1.15	0.65	1.2	0.6	1.15
	Kiki	1.15	0.9	0.6	0.35	1.15
	Amare*	1.3	1.2	0.55	0.0	1.2

*Juvenile **Mindy's values for digit 2 excluded from analyses. Middle phalanx does not make contact with ground surface.

Table 2.3: Results of paired T-test examining peak pressures of digit 2-5. Analysis included adults only.

Genus	Individual	D2-D3	D2-D4	D2-D5	D3-D4	D3-D5	D4-D5
Pan	Kira	**	**	**	NS	**	**
	Brandy	NS	NS	**	NS	**	**
	Mindy				NS	*	**
	Jadine	NS	NS	*	NS	**	**
	Candy	NS	NS	NS	NS	NS	NS
	Apollo	*	NS	NS	*	**	NS
Gorilla	Bulera	NS	NS	NS	NS	*	NS
	Medini	*	NS	*	*	**	*
	Kwan	NS	NS	NS	NS	NS	NS
	Gigi	NS	NS	NS	NS	NS	NS
	Okie	NS	NS	NS	NS	NS	NS
	Joe	NS	NS	NS	NS	NS	NS
	Kiki	NS	NS	NS	NS	NS	NS

*P<0.05 **P<0.001 NS=Not significant D# = Digit #

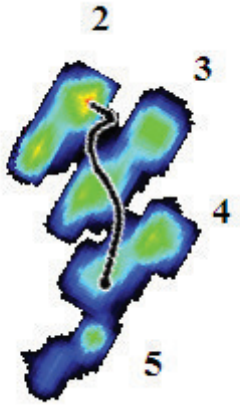

Figure 2.1: Pressure distribution output of the right hand of a female chimpanzee. Hand is oriented in the palm-in position. Initial contact is made with digit 5 and the center of pressure (black line) moves towards 2. Final touch-off and maximum pressure occurs at digit 2.

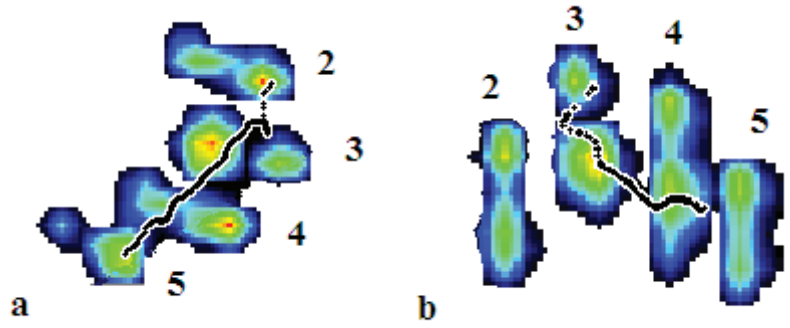

Figure 2.2: Pressure distribution outputs of the right hand of a male chimpanzee. Touch-off and maximum pressure is at digit 2 in the palm-in position (a.) and digit 3 in the palm-back position (b).

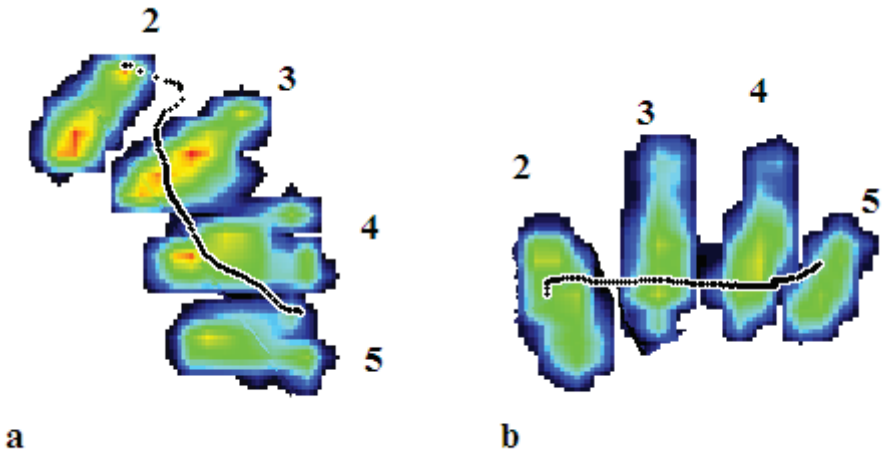

Figure 2.3: Pressure distribution outputs of the right hand of a female gorilla. Touch-off and maximum pressure occurs at digit 2 in both hand positions. (a) palm-in (b) palm-back

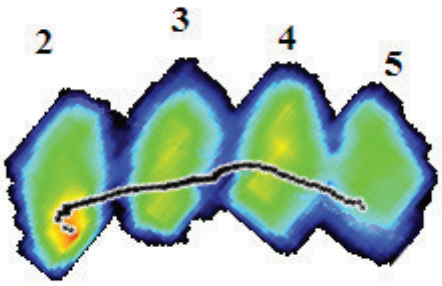

Figure 2.4: Pressure distribution output of the right hand of an adult male gorilla in the palm back position. Touch-off and maximum pressure occurs at digit 2. No prints of adult male silverbacks were in the palm-in position.

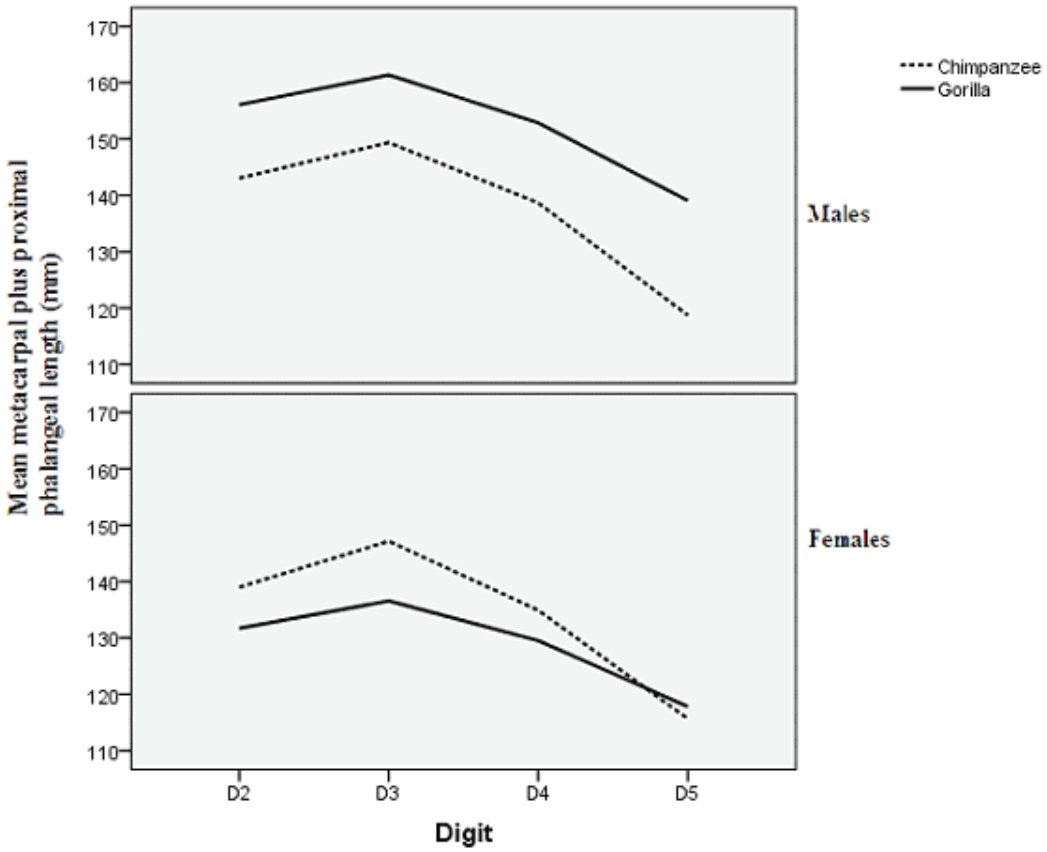

Figure 2.5: Mean values of metacarpal plus proximal phalangeal lengths for chimpanzee and gorilla males and females. Gorillas show a "flatter" pattern indicating less variability between digits 2-5.

CHAPTER 3

MANUAL PHALANGEAL CURVATURE AND KNUCKLE WALKING IN AFRICAN APES

Abstract

The morphology of primate manual phalanges is directly affected by the loads inflicted during locomotion. The degree to which these elements are curved has been used to infer the use of suspensory or non-suspensory locomotion in primates. Matarazzo (2008) constructed an index comparing the curvature values of the middle and proximal phalanges of digit 3 (the Index of Relative Curvature) to differentiate knuckle walkers from quadrupeds and brachiators. This index worked well for extant species, but its applicability to the fossil record remained untested. Given the infrequency with which phalanges are recovered in the fossil record and the difficulty of assigning such elements to the proper digits or individuals, it must be determined if the locomotor signal seen within digit 3 also exists: (1). in other rays, (2). when elements belonging to different rays of the same hand are used in the comparison, and (3). when elements belonging to different individuals of the same species are compared. The present study extends previous analysis by examining the relative curvature of the proximal and middle phalanges of digits 2, 4 and 5, in addition to 3. The study includes knuckle-walking (*Pan troglodytes* and *Gorilla gorilla*), quadrupedal (*Macaca fascicularis, M. nemestrina* and *Sapajus apella*), and suspensory (*Pongo pygmaeus*, *Hylobates lar*, and *Ateles* spp.) primates. The Indices of Relative Curvature composed of elements from a single ray, and those indices derived from curvature values of middle and proximal phalanges of

different rays (2-5) are both successful in discriminating between locomotor categories. Indices comprised of elements from different individuals have means similar to those indices derived from proximal and middle phalanges of the same individual's ray. This suggests that Indices of Relative Curvature can be applied successfully to fossils and other cases for which digit identity cannot be ascertained, and for which isolated proximal and middle phalanges may not belong to a single digit.

Introduction

The transition from quadrupedalism to bipedalism in the hominin lineage has been the subject of considerable debate (Begun, 1993; Shea and Inouye, 1993; Dainton and Macho, 1999; Corruccini and McHenry, 2001; Dainton, 2001; Kelly, 2001; Lovejoy et al., 2001; Richmond and Strait, 2000, 2001a, b; Richmond et al., 2001; Inouye and Shea 2004; Kivell and Schmitt 2009; Williams 2010). Did this transition involve a knuckle-walking phase, or was the pre-bipedal ancestor of modern humans more suspensory? Past research on the morphology of the manual phalanges and wrists of extant primates and early hominins has not provided a resolution to this debate. This paper examines the curvature of both the proximal and middle manual phalanges of digits 2-5 in an attempt to provide an alternative source of information. While proximal phalangeal curvature has been linked biomechanically to suspensory behaviors in primates, middle phalangeal curvature has yet to receive significant scrutiny. Phalangeal curvature has been shown to be epigenetically sensitive to variation in locomotor behavior (Richmond, 1998) and thus to confer evidence of lifetime activity patterns making it an effective tool for paleontological inference. The curvature of the proximal

phalanges of the manus of primates varies in conjunction with levels of suspension (Susman, 1979; Richmond, 1998; 2007; Jungers et al., 1994; 1997; 2002). Using finite element analysis, Richmond (1998; 2007) showed that strain magnitudes are lower in the highly curved manual proximal phalanges of siamangs under suspension than they would be, under similar loading conditions, if those same phalanges were straight. This implies that the high stresses generated during gripping and manual flexing in arboreal settings are resisted by some measure of phalangeal curvature (Jungers et al., 2002). Ontogenetic studies of the proximal phalanges of extant primates reveal that phalangeal curvature changes as the positional behavior of individuals change, most probably via bone modeling and remodeling in response to mechanical stresses (Richmond, 1998; 2007). Although the extent of curvature may be genetically limited, it is clear that a biomechanical signal is preserved within the proximal phalanges. However, ontogenetic and finite element studies of the manual middle phalanges have not been conducted. Thus, we do not know the extent to which manual middle phalanges are affected by a locomotor stresses. Matarazzo (2008) showed that taken alone, the middle phalanges of digit 3 are not successful at discriminating between locomotor categories.

During knuckle walking, the metacarpophalangeal (MCP) joints are in a hyperextended position and weight is borne primarily on the dorsal aspects of the middle phalanges of digits 2-4 (Tuttle, 1969; Marzke & Wullstein, 1996; Wunderlich & Jungers, 1998). Tuttle (1969) noted that the tensile forces placed on the digits during knuckle walking are largely ameliorated by ligaments and tendons which are “strengthened” when the hand is in the knuckle-walking position. This would leave compression as the main

force acting upon the middle phalanges. Thus, one would predict that the middle phalanges should be relatively straighter than the proximal phalanges to allow for increased ground-to-digit surface contact and greater dissipation of the compressive force along these elements (Richmond et al., 2001).

In the case of non-knuckle-walking digitigrade quadrupeds such as macaques, flattened middle phalanges are expected for entirely different reasons. Typically in digitigrade quadrupedalism, the MCP joints of digits 2-5 are hyperextended with the metacarpals held in a vertical position (Hayama et al, 1994). The palmar aspects of the distal phalanges are the primary contact with the substrate and the manual rays are held at an acute angle to the ground surface. Using finite element analyses of the proximal phalanges of patas monkeys and macaques, Richmond (1998) showed that, in terrestrial walking, straighter phalanges withstand high compressive joint reaction forces better than do curved phalanges. He also postulated that patas-like manual postures would be nearly impossible with highly curved phalanges, as they would require "an improbable degree of hyperextension" at the MCP joint (Richmond, 1998, p. 208).

Most primate species' middle phalanges are subject to forces similar to those experienced by the proximal phalanges and thus would be expected to show similar degrees of curvature. This is true for non-knuckle-walking quadrupeds for which lower degrees of curvature are expected for both proximal and middle phalanges and for more suspensory primates where one might expect high phalangeal curvature for both elements. Knuckle walkers, however, experience markedly different force regimes on the proximal and middle phalanges. Thus, different degrees of curvature should characterize

the proximal and middle phalanges. Matarazzo (2008) has shown, that the middle phalanges of digit 3 are flatter than the corresponding proximal phalanges. It is unclear however, if this pattern can be seen within the other digits due to noted differences in pressure application. Digits 2-5 experience different degrees of pressure applications during knuckle walking: digit 5 receives less pressure, and presumably less mechanical stress, than the other rays. Chimpanzees and gorillas apply pressure in a fairly similar manner across digits 2, 3, and 4 when knuckle walking (although minor differences exist between taxa) (Matarazzo, this dissertation, Ch. 2). Chimpanzees alter hand position more frequently from palm-back (hand facing posteriorly) to palm-in (hand facing toward body) which causes a shift in highest pressure point from digit 3 (palm-back) to digit 2 (palm-in). Individual chimpanzees are also more likely to apply no pressure to digits 2 or 5 in a given knuckle-walking bout (those digits are held in a flexed position and do not make any ground contact). In contrast, gorillas utilize the palm-back hand posture consistently and make contact with all four digits 2-5 with greater frequency than chimpanzees. Terrestrial, quadrupedal olive baboons show an entirely different pressure pattern, one that varies in a consistent manner with speed (Patel and Wunderlich, 2010). Patel and Wunderlich (2010) showed that baboons make initial ground contact with the distal phalanges and only occasionally involved the middle and proximal phalanges during terrestrial locomotion. Ground contact shifts from the distal phalanges directly to the metacarpal heads. Increased palmar contact is made at higher velocities, and pressure is consistently highest in the palmar region near the metacarpal heads of digits 3 and 4. Both pressure studies show that the least amount of pressure is placed upon digit 5.

In general, the pollex (digit1) is easily discernable in the fossil record and not consistently used by different taxa during terrestrial locomotion so it is not considered in the following analyses. The elements of digit 5, however, can be more difficult to distinguish and do experience pressure (albeit lightly) and thus will be included in all examinations.

A prior study (Matarazzo, 2008) of the relative curvature of the proximal and middle phalanges of the third digit of chimpanzees, gorillas, capuchins, spider monkeys, orangutans, gibbons and macaques succeeded in identifying differences between knuckle walkers, brachiators, and non-knuckle walking quadrupeds using an "Index of Relative Curvature" (middle phalangeal curvature/proximal phalangeal curvature). Brachiators have relatively equal proximal and middle curvature values and thus index values approximating 1.0; quadrupeds have greater curvature in the middle phalanges than proximal, and thus indices greater than 1.0, and knuckle walkers possess flatter middle phalanges and curved proximal, and thus indices considerably lower than 1.0 (~0.85). This study focused solely on the third manual ray.

The following dissertation chapter examines the proximal and middle phalanges of digits 2-5 to see if the locomotor signal displayed by digit 3 also holds for the other manual rays. Given the sparse nature of the fossil record in which discovery of corresponding phalanges from a single digit is rare, an examination of indices composed of elements from different rays is also conducted.

Samples and Methods

Phalangeal curvature of digits 2-5 was assessed for 234 individuals representing four locomotor categories: knuckle walkers (*Pan* and *Gorilla*), quadrumanous climbers (*Pongo*), brachiators (*Ateles* and *Hylobates*), and quadrupeds (*Sapajus* and *Macaca*) (Table 3.1). Individuals were included in the sample if epiphyses on all manual skeletal elements were fused and if both the proximal and middle phalanges for each digit were present. Phalangeal curvature was measured using the procedure outlined in Jungers et al. (1997); this method was used previously to assess curvature in the third ray (Matarazzo, 2008). Curvature values are calculated based on three measures: projected height (H), dorso-palmar midshaft diameter (D), and interarticular length (L) (Figure 3.1). These measures are used to calculate the radius of curvature (R) using the following equation:

$R = [(H - D/2)^2 + (L/2)^2]/[2(H - D/2)]$.

The angle of curvature (theta θ) is calculated with the following equation:

$\Theta = 2 * \arcsin(L/2R)$.

The resulting angle is converted from radians to degrees by multiplying by 57.295. To capture the relationship between curvatures of the proximal (Px) and middle (Md) phalanges of each manual digit, an Index of Relative Curvature (Md curvature/Px curvature) was calculated.

Degrees of curvature for both the proximal and middle phalanges and Indices of Relative Curvature (IRC) were analyzed using SPSS statistical software Version 20.0.

Given the size disparity between male and female gorillas and the individual variation in pressure output noted in chimpanzees (Matarazzo, this dissertation, Chapter 2), t-tests were used to assess differences between sexes for proximal and middle phalangeal curvature, as well as the Indices of Relative Curvature for corresponding digital elements. ANOVAs with Tukey's HSD were also used to check for significant differences between genera for proximal and middle phalangeal curvature values and Indices of Relative Curvature. Within-manus comparisons were also analyzed using a general linear model with Tukey's post hoc tests of honestly significant differences.

Curvature profiles, i.e. the pattern of highest to lowest phalangeal curvature (md and px) within a manus, was determined for each taxon. This is a description of variation across the manus. These profiles were qualitatively compared between taxa to determine if there were similarities between taxa assigned to the same locomotor category.

Indices of Relative Curvature were also calculated using non-corresponding elements of rays 2-5; for example, the middle phalanx of digit 2 (md2) might be divided by proximal phalanx of digit 3 (px3). This would be designated "IRC md2/px3". Differences between locomotor categories for these indices were assessed using Tukey's HSD.

A discriminant function analysis (DFA) was run to determine whether genera that differ most from each other also belong to different locomotor groups. Locomotion was not included as a variable; rather the IRC scores of corresponding and non-corresponding

digits were used to discriminate among taxa and the DFA function scores were saved. Euclidean distances between genus centroids for those function scores were subsequently also generated to test the hypothesis that IRC scores really do distinguish among species belonging to different locomotor "groups". Anova with Tukey's HSD was run to assess differences in IRC scores of corresponding and non-corresponding elements between locomotor categories.

Bootstrapping analysis (in which IRC values were constructed by combining middle and proximal curvature values taken from *any* two individuals, male, female, or both, was conducted for each taxon. One thousand iterations of each index were produced. Resulting distributions were compared with the distributions created from corresponding elements and to those created from non-corresponding elements within individual hands for each taxon.

Results

Basic Curvature and Index Values

Mean curvature values (degrees) for the middle and proximal phalanges are presented in Table 3.2. Indices of relative curvature were calculated for phalanges within the same ray (digits 2-5) (Table 3.3) and for middle and proximal phalanges of different rays from within the same manus for each taxon (Table 3.4).

Sex Differences

T-tests comparing the middle and proximal phalangeal curvature values and IRC scores of corresponding digital elements between the sexes revealed no significant

differences in *Ateles* spp, *Hylobates lar*, or *Macaca* spp. Only the larger bodied species, and occasionally *Sapajus*, show some significant differences between the sexes, but not in any consistent manner. *Pan troglodytes* males and females had significantly different values for IRC5 ($t = -2.92$, $df = 50$, $P = 0.006$); *Gorilla gorilla* males and females for IRC 2 ($t = -2.03$, $df = 83$, $P = 0.047$); and *Sapajus apella* males and females for IRC 4 ($t = -2.54$, $df = 9$, $P = 0.03$). *Pongo pygmaeus* males and females had no significant differences in IRC values but were significantly different for proximal phalangeal curvature of digit 3 ($t = 2.2$, $df = 35$, $P = 0.04$), middle phalangeal curvature of digits 2-5 (Md2: $t = 2.5$, $df = 34$, $P = 0.02$; Md3: $t = 2.8$, $df = 35$, $P = 0.008$; MD4: $t = 3.38$, $df = 35$, $P = 0.002$; MD5: $t = 2.9$, $df = 33$, $P = 0.007$).

Differences among Taxa for Individual Elements

Between taxon differences in the middle and proximal phalangeal curvature values do not show a pattern that can be correlated in a simple fashion with between-taxon differences in locomotion. ANOVAs with a Tukey's HSD reveal a number of significant differences between elements for included taxa (Tables 3.5 and 3.6). Orangutans have significantly higher proximal phalangeal curvature values for digit 2-5 than all other taxa, and significantly higher middle phalangeal values for digits 2-5 than chimpanzees and gorillas and digits 2-4 for macaques, capuchins, and gibbons. Chimpanzees have significantly greater proximal phalangeal curvature than capuchins and macaques, but are not significantly different from these taxa for middle phalangeal curvature values. Gorillas have significantly greater proximal phalangeal curvature than

chimpanzees for digits 2-5 but do not differ from them in middle phalangeal curvature values.

The curvature profiles differ by taxon, except for chimpanzees and gorillas, which exhibit identical patterns. In addition, the most suspensory taxa have similar although not identical digit curvature profiles. For chimpanzees and gorillas, proximal and middle phalangeal curvature is greatest in digit 5 and decreases in the following pattern for the proximal phalanges: Px5> Px2> Px4> Px3; and for middle phalanges: Md5> Md2> Md3> Md4. The middle phalanges of digits 3 and 4, which bear substantial weight during knuckle walking, are the least curved (Matarazzo, this dissertation, Chapter 2). The most suspensory apes, gibbons and orangutans, have different phalangeal patterns but both have greatest middle phalangeal curvature on digits 3 and 4 and least on digits 2 and 5 (gibbons Md4 > Md3 > Md5 > Md2; orangutans Md3 > Md4 > Md2 > Md5). The knuckle walkers have significantly flatter middle phalanges than the more suspensory apes (Table 3.7).

Within-manus Differences

The curvature and IRCs for digits 2-5 for non-knuckle-walking taxa are similar across the manus. Knuckle-walking taxa show a similar pattern of curvature that is not seen in other taxa. A Tukey's test of Honestly Significant Differences comparing the phalangeal curvature values and IRC values of digits 2-5 revealed no significant differences between the rays for *Pongo*, *Sapajus*, and *Hylobates*. The digits of *Pan* did not differ significantly in their proximal phalangeal curvature values. Significant

differences among digits were seen in the middle phalangeal values and IRC scores, specifically, homogeneous subsets for chimpanzee group digits 3 and 4 (subset 1) and digits 2 and 5 (subset 2) for both middle phalangeal and IRC values respectively (Table 3.8). *Gorilla* shows a similar pattern for middle phalangeal curvature values: digits 2 and 5 (subset 2) have significantly greater curvature than digits 3 and 4 (subset 1) (Table 3.9). However, there is considerable overlap in proximal phalangeal curvature values and IRC scores for these taxa: digits 3 and 4 comprise subset 1, and digits 3, 2, and 5 are within subset 2. Digit 5 has significantly greater *proximal* phalangeal curvature than digit 3 ($P = 0.027$, $SE = 0.70$), and digit 4 of *Gorilla* has a significantly lower IRC score than those of 2 and 5 ($P < 0.001$, $SE = 0.01$). Both *Macaca* and *Ateles* show no significant difference between the rays for proximal and middle curvature values. However, in *Macaca* digit 4 has a significantly lower IRC score than digit 5 ($P = 0.024$, $SE = 0.04$), and for *Ateles*; digit 3 has a significantly lower IRC score than digit 5 ($P = 0.029$, $SE = 0.04$).

Locomotor and Taxon Differences

Functions 1 and 2 of the discriminant function analysis run to distinguish among taxa using IRC scores comprised from corresponding and non-corresponding elements were statistically significant ($P < 0.001$). All raw variables were highly positively correlated with Function 1. Several indices showed a negative correlation with Function 2 (md4/px5, md3/px5, md4/px2, and IRC4). Function 1 accounts for 81.7% of total variance and Function 2 for 9.5%. The DFA correctly classified 66.2% of the original grouped cases. Function 1 polarizes, on the one hand, macaques and capuchins (with positive scores) and chimpanzees, gorillas, and orangutans (with negative scores).

Gibbons and spider monkeys lie between these groups along Function 1. The Euclidean distances between group centroids for Functions 1 and 2 show that taxa attributed to the same locomotor categories based on behavioral research are indeed closer to one another than to taxa belonging to different locomotor groups (Table 3.10). The centroids of *Pan*, *Gorilla*, and *Pongo* are closer to each other than to any of the other taxa; with *Pan* and *Gorilla* closer to one another than either is to *Pongo*. The placement of *Pongo* near the knucklewalkers is a function of them having similar values for the indices but as shown above, they have significantly greater phalangeal curvature values than *Pan* and *Gorilla*. The centroids of quadrupeds *Macaca* and *Sapajus* are relatively close to one another; however, they are also not far from *Hylobates*. The centroids of *Hylobates* and *Ateles* are closer to one another than to any other included taxon. The close proximity of the centroids of *Hylobates* and *Ateles*, and also the close proximity of the centroids of *Sapajus* and *Macaca* is a strong indication of a functional signal given the phylogenetic distance between the two genera in each pairing.

An ANOVA with Tukey's test of HSD was also run to compare the IRC scores of assigned locomotor categories. The IRC scores from corresponding and non-corresponding elements revealed significant differences between locomotor groups (F values range from 42.4 to 97.3; $P < 0.001$) (Tables 3.11-3.13). All locomotor groups differed significantly in their IRC scores for digit 3. The IRC scores for digits 2 and 5 were significantly different for all locomotor categories except knuckle walkers and quadrumanous climbers. IRC 4 did not differ significantly for quadrupeds vs. brachiators. Knuckle walkers and quadrumanous climbers do have significantly different

IRC values for 56% of the indices derived from corresponding and non corresponding elements (Tables 3.11 and 3.14). Quadrupeds are distinguished from all other locomotor categories in all IRC scores with the exception of brachiators. Quadrupeds and brachiators have similar values for IRC4, Md4/Px2, Md3/Px5, and Md4/Px5. Although not every index is capable of discriminating between all locomotor categories, we see significant differences in a number of them. Knucklewalkers are successfully differentiated from quadrupeds and brachiators with every included index (Table 3.14).

Bootstrapping conducted for each IRC score (of corresponding and non-corresponding elements) for each taxon resulted in means that did not differ significantly from those index values created from within an individual's own manus (see Appendix 2).

Discussion

The analyses reported here reveal that the knuckle walkers do indeed possess relatively straight middle phalanges as compared to their corresponding proximal phalanges for digits 2-5. The knuckle walkers included in this study (*Pan troglodytes*, *Gorilla gorilla gorilla* and *G. g. beringei*) frequently travel terrestrially via knuckle walking, but also spend varying amounts of time using suspensory postures (Tuttle, 1969; Inouye, 1994; Doran, 1997). During knuckle walking, the ground surface is contacted by the dorsal surfaces of the middle phalanges placing a considerable amount of compressive force onto the middle phalanges. Thus it was expected that these elements

will be relatively straight allowing weight to be distributed across the middle phalanges during locomotion.

Gorillas display a different pattern of weight distribution than chimpanzees when knuckle walking. Digits 2-5 all contact the surface when gorillas knuckle walk. However, weight appears to be placed primarily on the dorsal surfaces of the 2 and 3 middle phalanges (Tuttle, 1969; Inouye, 1994, Matarazzo, 2008, this dissertation, Chapter 2). In contrast, common chimpanzees emphasize digits 3 and 4, and occasionally keep digit 2 flexed so that it may only lightly contact a substrate (Tuttle, 1969; Inouye, 1994). Chimpanzees vary considerably in hand and digit posture when knuckle walking, whereas gorillas consistently contact the ground surface with digits 2-5 and maintain their hands in a fully pronated position while knuckle walking (Tuttle, 1969, Matarazzo, this dissertation, Chapter 2).

Chimpanzees possess an interesting profile of curvature across the manus; Digit 2 has a similar IRC value to digit 5, and 3 to digit 4. This same pattern has been noted with the absolute lengths of these digits (metacarpals plus proximal phalanges). Digits 3 and 4 are longer than 2 and 5 creating an "uneven platform" for knuckle walking (Matarazzo, this dissertation, Chapter 2). During knuckle walking, weight is preferentially placed on these digits and individuals may not even make contact with digits 2 or 5 (Matarazzo, this dissertation, Chapter 2). Gorillas display a different pattern whereby there is a greater similarity in IRC scores with digit 3 grouping with 4 and digit 3 with digits 2 and 5. This pattern is also seen with the lengths of the rays giving gorillas a more even knuckle-

walking platform. Other included taxa (gibbons, spider monkeys, macaques, capuchins, and orangutans) display similar IRC values for digits 2-5 alluding to more even distribution of locomotor forces across the manus in these primates as well. When the middle phalangeal curvature values are examined across the manus, chimpanzees and gorillas are the only two taxa that have the *same* pattern of curvature. Digits 5 and 2 are most curved and digits 3 and 4 are least curved. Digits 3 and 4 are frequently used as "touch-off" digits during a knuckle-walking stride and receive greater amounts of pressure than the lateral rays (Matarazzo, this dissertation, Chapter 2). The other apes, orangutans and gibbons do not share a curvature pattern across the hand but both have greater curvature on digits 3 and 4. These two digits (3 and 4) form the midline of the hand and may experience greater forces during suspensory postures.

The discriminant function and Tukey's analyses revealed similarities in the IRC values of knuckle walkers and quadrumanous climbers. Similar results were also noted in the original comparison of the IRC values for digit three (Matarazzo 2008). Whereas the great apes do have similar IRC values, the structure of the rays are actually quite different. The lower (~0.85) IRC scores of the knuckle walkers reflect their "flattened" middle phalanges (curvature of ~48˚) coupled with more curved proximal phalanges (~55˚). In contrast, orangutans have significantly higher curvature values in both elements but the proximal (~64˚) exceeds the middle (~58˚). The flattened state of the middle phalanges of the knuckle walkers is hypothesized to allow for greater contact of the knuckle-walking surface and therefore enhanced dissipation of force along the manus. High curvature values like those noted in the orangutan and brachiators have been shown

to be biomechanically more efficient during suspension by reducing stress along these elements (Richmond, 1998). Several of the IRC values composed of non-corresponding digital elements were capable of discriminating between all locomotor categories including knuckle walkers and quadrumanous climbers.

Like the knuckle walkers, capuchins and macaques do not display comparable proximal and middle curvature values. They possess relatively straight proximal phalanges and moderately curved middle phalanges, and therefore Indices of Relative Curvature greater than 1.0. This phalangeal pattern was not initially expected for these quadrupedal primates. It was predicted that their middle and proximal phalanges would experience similar forces during locomotion and thus show similarly low curvature values. As these taxa use arboreal substrates at least some of the time (Rodman, 1979; Cant, 1988; Burr et al., 1989; Garber and Rehg, 1999) their *relatively* high middle phalangeal curvature values may reflect the biomechanical constraints of gripping substrates, or more likely, climbing and infrequent use of suspension. Analyses also reveal that the relatively small-bodied, highly suspensory taxa (*Ateles* spp. and *Hylobates lar*) share a suite of phalangeal characteristics, including similar values for proximal phalangeal curvature, middle phalangeal curvature, and the Index of Relative Curvature. Both groups display relatively high values for proximal (second only to those of *Pongo pygmaeus*) and middle phalangeal curvature, giving them Relative Curvature values that approximate 1. Both practice a form of fluid brachiation and possess long curved digits 2-5 and a reduced pollex (Garber and Rehg, 1999; Chang et al., 2000; Cant et al., 2001; 2003; Tague, 2002; Youlatos, 2002; Usherwood et al., 2003). Both inhabit tropical rain

forests with diverse vegetation, and in any given brachiation bout they may be required to adjust to different superstrate diameters, shapes, slopes, and heights (Bertram, 2004). Differences in forest structure may explain a wide range of observed variation in the phalangeal curvature values within this group, but more research is needed to test such hypotheses.

Pongo pygmaeus displays high degrees of both proximal and middle phalangeal curvature in all four digits 2-5 which are significantly greater than those seen in the knuckle walkers. Due to the extremely high curvature of their proximal phalanges relative to the marked curvature of their middle phalanges, their values for the Index of Relative Curvature are comparable to those of knuckle walkers, and significantly different from the small-bodied agile brachiators (*Ateles* spp. and *Hylobates lar*) with whom they were expected to group on the basis of their high degree of suspension. However, although they are highly suspensory, *Pongo pygmaeus* does not practice locomotor patterns similar to those of the agile brachiators. Their primary mode of locomotion has been described as quadrumanous climbing which is characterized by use of both hands and feet to grip branches as they move deliberately through the canopy (Tuttle and Cortright, 1988). What must be emphasized here is that *Pongo pygmaeus* can be distinguished from knuckle walkers when the Indices of Relative Curvature and absolute proximal phalangeal curvature values are taken into consideration (Matarazzo, 2008). They also display a pattern of curvature across the manus that differs from the African apes. Both chimpanzees and gorillas have relatively greater curvature on the

middle phalanges of digits 2 and 5 and less on digits 3 and 4, while orangutans show an opposite pattern whereby the central digits (3 and 4) have increased curvature.

The existence of a clear knuckle-walking "signal" in the skeletal anatomy of the hand may prove to be useful given the ongoing debate concerning knuckle walking in hominin evolution (Begun, 1993; Shea and Inouye, 1993; Dainton and Macho, 1999; Corruccini and McHenry, 2001; Dainton, 2001; Kelly, 2001; Lovejoy et al., 2001; Richmond and Strait, 2000, 2001a, b; Richmond et al., 2001). This might open a new venue for understanding the evolution of hominoid locomotion – one that centers appropriately on those very elements of the hand that can be expected to have supported body mass during ground locomotion in knuckle walkers.

Most notably, those indices composed of non-corresponding elements were as successful at differentiating between locomotor groups as those composed of corresponding elements of the same digit. Also bootstrapped data in which indices were composed of elements from *any* individual within a species were not significantly different from indices composed of elements from within a single manus. For fossils, recovering a complete digit is rare. The ability to use non-corresponding middle and proximal phalanges (even from different individuals) and still sort reliably between categories is an invaluable tool.

Conclusions

Past studies of the manual proximal phalanges have revealed a relationship between degree of suspension and phalangeal curvature, with highly suspensory animals

possessing the most curved proximal phalanges. This study supports this relationship for the proximal phalanges of digits 2-5 and confirms the existence of the same tendency in the middle phalanges (Table 3. 15).

Highly suspensory *Hylobates lar*, *Ateles* spp., and *Pongo pygmaeus* show considerable curvature of both proximal and middle phalanges, knuckle walkers possess relatively straight middle phalanges and curved corresponding proximal phalanges, and non-knuckle-walking quadrupeds have relatively curved middle phalanges and straighter proximal phalanges. These differences are consistent with expectations based on the locomotor repertoires of these primates. Knuckle walkers, in particular, place a considerable amount of compressive force onto their middle phalanges while knucklewalking, and straighter middle phalanges allow for greater phalangeal surface contact with the ground and more even distribution of weight throughout these elements.

In addition I show that the Indices of Relative Curvature for corresponding elements of the same ray, from non-corresponding phalanges within the manus, and from elements of different individuals provide a functional signal not accessible from either the proximal or middle phalanges alone, that distinguishes knuckle walkers from other quadrupeds as well as from highly suspensory species. Knuckle walkers (*Pan troglodytes*, *Gorilla gorilla*) have relatively little curvature of the middle phalanges coupled with marked curvature of the proximal phalanges (but not as marked as in *Pongo pygmaeus*). The successful discrimination of locomotor groups with indices derived from

different individuals of the same species is particularly useful in the examination of fossil elements where attribution of a phalanx to a particular individual or ray can be difficult.

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Table 3.1. Sample sizes by sex

Genus and species	# Males	# Females	Total	Locomotion
Gorilla gorilla	59	28	87	Knuckle walker
Pan troglodytes	35	18	53	Knuckle walker
Pongo pygmaeus	15	22	37	Quadrumanus climber
Hylobates lar	9	6	15	Brachiator
Ateles spp.	3	9	12	Brachiator
Macaca spp.	8	11	19	Quadruped
Sapajus apella	5	6	11	Quadruped

Table 3.2. Middle and phalangeal curvature means (in degrees) for included genera.

Genus and species	Px2	Px3	Px4	Px5	Md2	Md3	Md4	Md5
Gorilla gorilla	56.5	55.5	55.9	57.3	48.7	46.4	44.9	49.4
Pan troglodytes	52.7	52.1	52.7	54.1	48.6	45.2	45.1	50.4
Pongo pygmaeus	62.4	64.3	65.4	62.8	56.6	58.0	57.3	55.3
Hylobates lar	51.5	55.5	53.8	54.9	55.1	56.4	59.4	55.8
Ateles spp.	49.3	55.5	50.8	47.7	49.8	49.5	50.4	51.6
Macaca spp.	44.9	44.2	46.2	44.6	50.2	48.0	47.6	52.0
Sapajus apella	39.5	40.0	38.6	41.9	49.8	48.5	50.6	53.5

Px = Proximal phalanx, Md = Middle phalanx

Table 3.3. Index of Relative Curvature means for taxa.

Taxa	IRC 2	IRC 3	IRC 4	IRC 5
Gorilla g. gorilla	0.86	0.84	0.8	0.87
G. g. beringei	0.9	0.85	0.84	0.85
Pooled *Gorilla gorilla*	**0.86**	**0.84**	**0.81**	**0.86**
Pan troglodytes	0.93	0.87	0.86	0.94
Pongo pygmaeus	0.91	0.91	0.9	0.89
Hylobates lar	1.07	1.02	1.11	1.02
Ateles spp.	1.02	.98	1.0	1.11
Macaca fascicularis	1.16	1.07	1.04	1.2
Sapajus apella	1.27	1.22	1.32	1.29

Table 3.4. Average "Index of Relative Curvature" scores for each taxon for non corresponding digital elements.

Taxa	Md2 /Px3	Md2 /Px4	Md2 /Px5	Md3 /Px2	Md3 /Px4	Md3 /Px5	Md4 /Px2	Md4 /Px3	Md4 /Px5	Md5 /Px2	Md5 /Px3	Md5 /Px4
Gorilla gorilla	0.88	0.87	0.85	0.82	0.83	0.81	0.80	0.81	0.79	0.88	0.89	0.89
Pan troglodytes	0.94	0.93	0.91	0.87	0.86	0.84	0.86	0.87	0.84	0.97	0.98	0.96
Pongo pygmaeus	0.88	0.88	0.91	0.94	0.91	0.93	0.92	0.89	0.92	0.89	0.86	0.87
Hylobates lar	0.99	1.02	1.01	1.1	1.05	1.03	1.16	1.07	1.09	1.07	.99	1.03
Ateles spp.	0.99	1.0	1.08	1.0	.98	1.04	1.03	1.0	1.07	1.05	1.03	1.02
Macaca fascicularis	1.16	1.07	1.13	1.08	1.05	1.08	1.08	1.09	1.08	1.17	1.18	1.14
Sapajus apella	1.22	1.29	1.22	1.24	1.26	1.15	1.3	1.28	1.2	1.37	1.35	1.4

Table 3.5: Significant differences between proximal phalangeal curvature (Px) across taxa.

Taxa	*Gorilla*	*Pongo*	*Hylobates*	*Ateles*	*Macaca*	*Sapajus*
Pan	**Px2 **Px3 **Px4 **Px5	**Px2 **Px3 **Px4 **Px5		 **Px5	**Px2 **Px3 **Px4 **Px5	**Px2 **Px3 **Px4 **Px5
Gorilla		**Px2 **Px3 **Px4 **Px5	**Px2 **Px3	**Px2 **Px3 **Px4 **Px5	**Px2 **Px3 **Px4 **Px5	**Px2 **Px3 **Px4 **Px5
Pongo			**Px2 **Px3 **Px4 **Px5	**Px2 **Px3 **Px4 **Px5	**Px2 **Px3 **Px4 **Px5	**Px2 **Px3 **Px4 **Px5
Hylobates				 **Px5	**Px2 **Px3 **Px4 **Px5	**Px2 **Px3 **Px4 **Px5
Ateles					 **Px3	**Px2 **Px3 **Px4
Macaca						 **Px4

* P < 0.05 ** P < 0.001 Significantly higher values for taxon on the left are in bold (i.e. in row 1, *Pan* has significantly higher proximal phalangeal curvature values than *Ateles*, *Macaca* and *Sapajus* and significantly lower values than *Gorilla* and *Pongo*.)

Table 3.6: Significant differences between middle phalangeal curvature (Md) across taxa.

Taxa	*Gorilla*	*Pongo*	*Hylobates*	*Ateles*	*Macaca*	*Sapajus*
Pan		**Md2 **Md3 **Md4 **Md5	**Md2 **Md3 **Md4 **Md5	*Md4		*Md4
Gorilla		**Md2 **Md3 **Md4 **Md5	**Md2 **Md3 **Md4 **Md5	**Md4		**Md4
Pongo				**Md2** **Md3** **Md4**	**Md2** **Md3** **Md4**	**Md2** **Md3** **Md4**
Hylobates				**Md3** **Md4**	**Md3** **Md4**	***Md3** **Md4**
Ateles						**Md3**
Macaca						

* P < 0.05 ** P < 0.001 Significantly greater values are bolded. Unbolded values are significantly lower. (i.e. in row 1, *Pan* has significantly lower middle phalangeal curvature values than *Pongo*, *Hylobates*, *Ateles*, and *Sapajus*.)

Table 3.7. Middle phalangeal curvature homogenous subsets for hominoids.

		Md2		**Md3**		**Md4**		**Md5**	
Genus	**N**	Subset for alpha = 0.05		Subset for alpha = 0.05		Subset for alpha = 0.05		Subset for alpha = 0.05	
		1	2	1	2	1	2	1	2
Pan	52	48.6		45.2		45.1		50.4	
Gorilla	85	48.7		46.4		44.9		49.4	
Hylobates	15		55.1		56.4		59.4		55.8
Pongo	36		56.6		58.0		57.3		55.3
Sig.		1.0	0.74	0.79	0.57	1.0	0.37	0.88	0.98

Table 3.8: Chimpanzee homogenous subsets for middle phalangeal curvature values and IRC scores.

		Middle Phalangeal Curvature		**Index of Relative Curvature**	
Digit	**N**	Subset for alpha = 0.05		Subset for alpha = 0.05	
		1	2	1	2
Digit 4	52	45.1		0.86	
Digit 3	51	45.2		0.87	
Digit 2	52		48.6		0.93
Digit 5	51		50.5		0.94
Sig.		0.999	0.235	0.937	0.962

Table 3.9: Gorilla homogenous subsets for proximal and middle phalangeal curvature values and IRC scores.

		Proximal Phalangeal Curvature		**Middle Phalangeal Curvature**				**Index of Relative Curvature**	
Digit	N	Subset for alpha = 0.05		Subset for alpha = 0.05		Digit	N	Subset for alpha = 0.05	
		1	2	1	2			1	2
3	86	55.5		46.4		4	86	0.81	
4	86	55.9		44.9		3	86	0.84	0.84
5	85	56.5	56.5		49.5	5	83		0.86
2	83		57.5		48.7	2	84		0.86
Sig.		0.468	0.1	0.298	0.752			0.056	0.215

Table 3.10: Euclidean Distance (or Dissimilarity) Matrix based on scores generated by a genus-level discriminant function analysis.

Distance Matrix

	Euclidean Distance						
	Pan	*Gorilla*	*Pongo*	*Macaca*	*Sapajus*	*Hylobates*	*Ateles*
Pan	.000	1.040	1.528	3.765	6.417	3.751	2.588
Gorilla		.000	1.513	4.702	7.390	4.356	3.330
Pongo			.000	3.856	6.561	3.010	2.220
Macaca				.000	2.716	2.047	1.716
Sapajus					.000	4.190	4.369
Hylobates						.000	1.252
Ateles							.000

Table 3.11: Tukey's Honestly Significant Differences between knuckle walkers and other locomotor categories for IRC scores.

IRC Scores	Quadrumanous	Quadrupeds	Brachiators
IRC 2	P=0.83 SE=0.02 NS	* P<0.001 SE=0.03	* P<0.001 SE=0.03
IRC 3	* P=0.02 SE=0.02	* P<0.001 SE=0.02	* P<0.001 SE=0.02
IRC 4	* P=0.009 SE=0.02	* P<0.001 SE=0.02	* P<0.001 SE=0.02
IRC 5	P=0.999 SE=0.02 NS	* P<0.001 SE=0.02	* P<0.001 SE=0.02
Md2/Px3	P=0.74 SE=0.02 NS	* P<0.001 SE=0.03	* P=0.002 SE=0.03
Md2/Px4	P=0.97 SE=0.02 NS	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md2/Px5	P=0.48 SE=0.03 NS	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md3/Px2	* P<0.001 SE=0.02	* P<0.001 SE=0.02	* P<0.001 SE=0.02
Md3/Px4	* P=0.014 SE=0.02	* P<0.001 SE=0.02	* P<0.001 SE=0.02
Md3/Px5	* P<0.001 SE=0.02	* P<0.001 SE=0.02	* P<0.001 SE=0.02
Md4/Px2	* P<0.001 SE=0.02	* P<0.001 SE=0.02	* P<0.001 SE=0.02
Md4/Px3	* P=0.022 SE=0.02	* P<0.001 SE=0.02	* P<0.001 SE=0.02
Md4/Px5	* P<0.001 SE=0.02	* P<0.001 SE=0.02	* P<0.001 SE=0.02
Md5/Px2	P=0.86 SE=0.02 NS	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md5/Px3	* P=0.035 SE=0.02	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md5/Px4	P=0.138 SE=0.02 NS	* P<0.001 SE=0.03	* P<0.001 SE=0.03

Table 3.12: Tukey's Honestly Significant Differences between quadrumanous climbers and other locomotor categories for IRC scores.

IRC Scores	Quadrupeds	Brachiators
IRC 2	* P<0.001 SE=0.03	* P<0.001 SE=0.03
IRC 3	* P<0.001 SE=0.02	* P<0.001 SE=0.02
IRC 4	* P<0.001 SE=0.03	* P<0.001 SE=0.03
IRC 5	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md2/Px3	* P<0.001 SE=0.03	* P=0.001 SE=0.03
Md2/Px4	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md2/Px5	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md3/Px2	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md3/Px4	* P<0.001 SE=0.03	* P=0.001 SE=0.03
Md3/Px5	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md4/Px2	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md4/Px3	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md4/Px5	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md5/Px2	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md5/Px3	* P<0.001 SE=0.03	* P<0.001 SE=0.03
Md5/Px4	* P<0.001 SE=0.03	* P<0.001 SE=0.03

Table 3.13: Tukey's Honestly Significant Differences between qaudrupeds and brachiators for IRC scores.

IRC Scores	Brachiators
IRC 2	* P<0.001 SE=0.03
IRC 3	* P<0.001 SE=0.03
IRC 4	P=0.118 SE=0.03 NS
IRC 5	* P<0.001 SE=0.03
Md2/Px3	* P=0.001 SE=0.03
Md2/Px4	* P=0.001 SE=0.03
Md2/Px5	* P=0.005 SE=0.04
Md3/Px2	P=0.063 SE=0.03 NS
Md3/Px4	* P=0.035 SE=0.03
Md3/Px5	P=0.096 SE=0.03 NS
Md4/Px2	P<0.178 SE=0.03 NS
Md4/Px3	* P<0.001 SE=0.03
Md4/Px5	P=0.631 SE=0.03 NS
Md5/Px2	* P<0.001 SE=0.03
Md5/Px3	* P<0.001 SE=0.03
Md5/Px4	* P<0.001 SE=0.03

Table 3.14: Percentage of significantly different IRC scores for Tukey's Honestly Significant Differences between locomotor groups.

	Quadrumanous Climbers	Quadrupeds	Brachiators
Knuckle walkers	56%	100%	100%
Quadrumanous climbers		100%	100%
Quadrupeds			75%

Table 3.15 Summary table of expected and observed manual phalangeal curvature values for locomotor categories

Locomotor Categories	**Expected**	**Observed**
Knuckle walkers	Flatter Middle Phalanges to allow for greater digit to ground contact. Curved Proximal Phalanges reflective of suspensory behavior.	Flatter middle phalanges and curved proximal palanges. Indices of Relative Curvature are less than one.
Quadrupeds	Relatively flatter middle and proximal phalanges.	Flatter proximal phalanges and relatively curved middle phalanges. Indices of Relative Curvature are greater than one.
Quadrumanous Climbers	Highly curved middle and proximal phalanges needed to mitigate strain during suspension.	Both phalanges are highly curved (greatest curvature values of any extant primate). Indices of Relative Curvature are less than one.
Brachiators	Highly curved middle and proximal phalanges needed to mitigate strain during suspension.	Both phalanges are highly curved. Proximal and middle phalangeal curvature values are approximately equal. Indices of Relative Curvature are approximately equal to one.

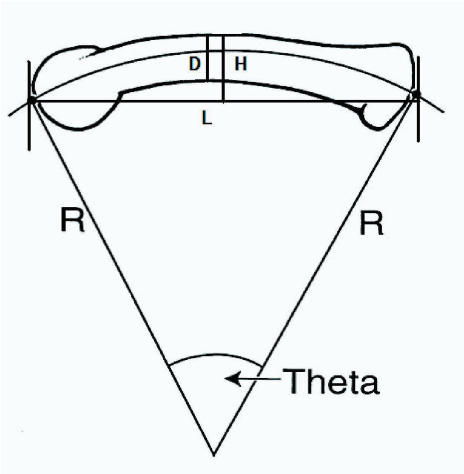

Figure 3.1: Curvature measurements: D depth, H height, L length, R radius of curvature (Image adapted from Jungers et al., 1997).

CHAPTER 4

TRABECULAR ARCHITECTURE OF THE MANUAL ELEMENTS

Abstract

Trabecular bone orientation has proven sensitive to loading patterns in the humerus and femur of primates. Because manual elements provide support during locomotion, differences in trabecular bone within the phalanges should be capable of discriminating between primates practicing different modes of locomotion. Micro CT scans of the middle phalanx, proximal phalanx and the metacarpal head of the third ray were used to examine the pattern of trabecular orientation in *Pan*, *Gorilla*, *Pongo*, *Hylobates* and *Macaca*. Several zones, i.e., the proximal ends of both phalanges and the metacarpal heads, were capable of distinguishing between knuckle-walking, quadrupedal and suspensory primates. Orientation and shape seem to be the primary distinguishing factors but differences in bone volume, isotropy index and degree of anisotropy were seen across included taxa. Suspensory primates show primarily proximodistal alignment of trabeculae in all zones, and quadrupeds more palmar-dorsal orientation in several zones. Knuckle walkers are characterized by having proximodistal alignment in the proximal ends of the phalanges and a palmar-dorsal alignment in the distal ends and metacarpal heads. Differences in orientation correlate with differences in strains placed upon the digits during locomotion: primarily compression in the middle phalanges and extension at the metacarpophalangeal joints during knuckle walking, and tensile forces during suspension.

Introduction

Living bone is a dynamic tissue that functionally adapts in response to mechanical loading. In addition to easily visible changes noted on the surface of bone, (i.e. bony deposits built up along heavily used muscle insertions and atrophy in areas of tissue damage and minimal use), it is widely accepted that changes in the internal structure of bone can be related to function. This adaptability of bone is commonly referred to as "Wolff's Law". Although the initial mathematical tenets of Wolff's law have been discredited (for an excellent review see Ruff et al., 2006), the ability of trabecular bone to align along a functional axis has been shown in several studies (Barak et al., 2011; Fox and Keaveny, 2001; Jacobs, 200; Keaveny et al., 2001; Mittra et al. 2205; Polk et al., 2008; Pontzer et. al, 2006). Pontzer et al. (2006) and Barak et al. (2011) empirically tested via animal studies the ability of trabecular bone to align along an axis of greater use. In the Pontzer et al. (2006) study, guinea fowl that were made to run on a treadmill at an incline had changes in the trabecular bone alignment of their distal femora that corresponded with the altered direction of load. These changes were not seen in control fowl running without an incline. Similar results were seen in the distal tibia of sheep that were made to run at an incline versus a control group (Barak et al., 2011). In addition to alignment alterations seen in the study sheep, they also noted significant increases in bone volume fraction (BV/TV), trabecular number (Tb.N), trabecular thickness (Tb.Th), and changes in trabecular shape (less rod-shaped) between the "inclined" group and control sheep.

With the advancement of technology, namely micro Computed Tomography (μCT) (employed in the above studies), it is now possible to examine the internal

structure of bone in finer detail and in three dimensions (Fajardo and Muller, 2001; Fajardo et al. 2002; Ketcham, 2005; Ketcham and Ryan, 2004; Ryan and van Rietbergen, 2005; Scherf and Tilgner, 2009; Waarsing et al., 2005). Micro CT scans have been used to examine changes in cortical bone thickness and shape, trabecular structure, and subchondral bone thickness mainly in primate long bones as a means to explore possible locomotor differences (DeSilva and Devlin, 2012; MacLatchy and Muller, 2002; Polk et al., 2010; Ryan and Ketcham, 2002; Ryan and Shaw, 2012; Ryan and Walker, 2010; Shaw and Ryan, 2012). The results of these analyses vary. While MacLatchy and Muller (2002) and Ryan and Ketcham (2002) revealed a relationship between femoral head trabecular orientation and locomotor patterns in several strepsirrhine species, this relationship does not seem to hold true for anthropoids. Trabecular structure alone (of the humeral and femoral heads) appears similar across a wide range of anthropoid primates and does not discriminate between locomotor groups (Ryan and Walker, 2010; Shaw and Ryan, 2012). Ryan and Walker (2010) did show that within the included anthropoids (*Alouatta*, *Pan*, *Papio*, *Presbytis*, and *Symphalangus*), the humeral head trabecular bone is more isotropic and has significantly lower bone volume than does femoral head trabecular bone. A stronger locomotor signal is manifest in the mid-diaphysis cortical bone of the femur and humerus across several anthropoids (Shaw and Ryan, 2012). This locomotor signal is also present when a *suite* of trabecular features are considered (Ryan and Shaw, 2012). Once body size is controlled, a suite of trabecular bone features of the femoral head (trabecular number, connectivity density, degree of anisotropy, and structure model index) discriminates well among locomotor categories.

The humeral head suite of features shows a similar but weaker locomotor signal (Ryan and Shaw 2012).

Micro CT analyses along with traditional histological preparations, morphometrics and CT osteoabsorptiometry (OAM) have also been employed to examine possible locomotor differences in the morphological structure of elements of the wrist and metacarpals of primates. Studies of the distal radius using CT-OAM revealed greater density in the subchondral bone of the ventral region in knuckle walkers that distinguishes them from humans, quadrupeds and orangutans (Carlson and Patel, 2006; Patel and Carlson, 2007). Greater density in this region is expected given the enhanced loading placed upon the area while the hand is in the knuckle-walking posture (with extension at the wrist and metacarpals). In contrast, digitigrade primates who keep the metacarpals in line with the wrist during the stance phase of walking exhibit the greatest density in the central region of the distal radius (Patel and Carlson, 2007). Zeininger et al. (2011) sectioned and imaged (using backscattered electron microscopy) the third metacarpal heads of *Pan*, *Pongo*, and *Homo* and revealed differences in weighted mean grey level patterns reflective of different digit use among the species: *Pan* has lighter grey levels in the dorsal and palmar regions indicating greater remodeling rates and loading at these zones. In his examination of cercopithecoid metacarpal shape (using morphometric measures), Patel (2010) showed a weak signal for hand posture and metacarpal morphology in cercopithecoids. Marchi (2005) however found differences in the cross-sectional properties of metacarpals 3 and 4 of hominoids that he related to locomotor function: namely, knuckle walkers had greater robusticity and strength of those digits than did orangutans and humans.

Micro CT studies of extant primate metacarpals have shown some inter- and intraspecific differences within hominoids. Chirchir et al. (2010) found that *Pan* had greater bone density in the dorsal region of third metacarpal head than *Pongo* and suggests this is due to greater loading of this region in chimpanzees during knuckle walking. Lazenby et al. (2011) examined the metacarpals (digits 1, 2, and 5) of *Pan* and noted differences in overall robusticity between Cameroon chimpanzees and those of the Tai forest. They attributed the greater robusticity of the Cameroon chimpanzee metacarpals to more frequent knuckle walking and/or greater tool use.

To date, nobody has studied the trabecular structure of the manual phalanges. Whereas it has been shown that the overall shape of phalanges is responsive to loads imposed during use, the internal structure of these elements has not been examined in this light. Increased manual proximal phalangeal curvature is a marker of suspensory behaviors in primates (Jungers et al., 1994; 1997; 2002; Richmond, 1998; 2007). Richmond (1998) has demonstrated how curvature increases throughout ontogeny with increased use of suspensory postures, and conversely how digits of infants (typically curved as they are used to grasp onto their mothers' fur) become increasingly flatter in quadrupedal primates as they age. Finite element analysis reveals how this curvature mitigates strain on the digits when they are loaded as if in suspension (Richmond 1998; 2007). A comparison of the curvature value of proximal and middle phalanges of the manus (Index of Relative Curvature) is successful at differentiating between quadrupedal, brachiating, quadrumanous, and knuckle-walking primates (Matarazzo, 2008; Chapter 3). This locomotor signal holds true even when the indices are comprised from middle and

proximal phalanges from different rays within the same manus, or with elements from different individuals of the same species. The Index of Relative Curvature reflects differences in how elements are loaded within a digit and across the locomotor spectrum. Knuckle walkers (*Pan* and *Gorilla*) have index values that approximate 0.85: the middle phalanges are "flatter" than the proximal and the inference can be made that these elements experience different angles of compression than the proximal phalanges when knuckle walking. In addition, when used in suspension, proximal phalanges experience tension in the palmar direction and compressive strain dorsally acting to "bend" the element (Richmond, 2007). Quadrupeds (*Macaca* and *Cebus*) may also experience different loads acting on the proximal and middle phalanges. They have index values greater than 1: the middle phalanges are more curved than the proximal. In contrast, the brachiators (*Hylobates* and *Ateles*) experience similar loads upon both the middle and proximal phalanges and possess index values approximately equal to 1. Both elements are highly curved and no significant differences in curvature values occur across the manus of individual brachiators indicating relatively even distribution of weight during locomotion. Quadrumanous climbers (orangutans) have indices that (like those of knuckle walkers) approximate 0.85. However, their middle phalanges are not flattened. They simply are not as curved as the proximal. Orangutans possess significantly higher middle and proximal curvature values than the other included taxa. Like brachiators, they have long, hook-like hands which may act to mitigate the considerable amount of tensile strain that may be placed upon the digits during suspension.

Given the markedly different forces applied to the manual digits in suspension, quadrupedalism and knuckle walking, one might expect to see distinct differences in trabecular bone alignment among species engaging in these types of locomotion. One caveat is that the proximal and middle phalanges may experience different loads depending on the position of the manus during movement. Also primates have broad locomotor repertories. Both *Pan* and *Gorilla*, frequently travel via knuckle walking but can spend considerable amounts of time climbing and in suspension. In addition, their hands are used for number of other tasks including grooming, tool making, and tool use. These require fine motor manipulation of the digits and may contribute to differences in manual morphology (Lazenby et al. 2011). Bearing this in mind, the positional behaviors of taxa included in this study (*Pan*, *Gorilla*, *Pongo*, *Hylobates*, and *Macaca*) differ in phalangeal curvature indices in a manner correlating with locomotion, and therefore it is expected that locomotor-related differences in trabecular orientation should also occur.

This paper examines the trabecular structure of the proximal and distal ends of manual middle and proximal phalanges and the metacarpal heads. The main goal is to determine whether there are features of the trabecular bone that can be related to locomotor function. The middle phalanges of knuckle walkers (*Pan* and *Gorilla*) experience considerable compressive forces as they support the body during knuckle walking, with pressure focused on the 2nd and 3rd digits (Matarazzo submitted; Chapter 2). Given this, I hypothesize that the middle phalanges will have a dorsal-palmar alignment of the trabecular bone. In contrast, the proximal phalanges of knuckle walkers experience downward compressive strain in the knuckle-walking position, but also tensile

force when the body is in a suspensory posture. These elements are expected to show a more proximodistal orientation of trabecular bone than the middle phalanges. The suspensory primates (*Pongo* and *Hylobates*) have substantial tensile and compressive forces acting on both the middle and proximal phalanges as they hang below branches and should display greater proximodistal trabecular orientation in both elements. Gibbons also experience torsional forces during their fluid and fast brachiation which can be altered within a give bout by branch diameter, distance, and height (Bertram and Chang, 2001; Chang et al., 2000; Usherwood et al., 2003), but it is unclear what affect this may have on trabecular structure. The quadrupeds (*Macaca*) may experience similar compressive forces on both elements if the hand is maintained in a fully palmigrade posture. It is expected that the main trabecular orientation for proximal phalanges will be palmar-dorsal and for the middle (more curved elements) proximodistal.

The metacarpal heads are loaded quite differently depending upon hand posture. Both knuckle walkers and arboreal quadrupeds can experience both tensile and compressive forces on these elements, while brachiators and quadrumanous climbers would be subjected primarily to tensile and possibly torsional forces during suspension. Previous studies (Chirchir et al., 2010; Zeininger et al., 2011) indicate greater loading in the dorsal and palmar regions of the metacarpal heads of knuckle walkers and it is expected that the trabecular bone will be aligned along this axis. In contrast, a proximodistal alignment is expected for the suspensory and quadrupedal primates. This is the first examination of trabecular bone in manual phalanges and greatly expands upon the previous examinations of the metacarpal head structure.

Methods

Taxa included in this study represent several locomotor categories: knuckle walkers (*Pan troglodytes* and *Gorilla gorilla*), quadrumanous climbers (*Pongo pygmaeus*), quadrupeds (*Macaca fascicularis*) and brachiators (*Hylobates lar*). Only adults were included in the study (Table 4.1). The third manual digit was chosen as it acts as the midline axis of the hand in all taxa and receives relatively greater pressure than the other digits during knuckle walking (Matarazzo Chapter 2).

The 3rd proximal phalanges, 3rd middle phalanges, and 3rd metacarpals were scanned using the HMXST Micro-CT imaging system, Harvard University. The apes were adult, wild-caught specimens (Museum of Comparative Zoology at Harvard) and the macaques were adult male captive animals (UMASS collection). The phalanges were scanned at 70kv 80ua (apes) and 50kv 80ua (macaques). Images were reconstructed with CT Pro software and exported as TIFF files from the VG Studiomax program.

Trabecular "cubes" were extracted using Irfanview and analyzed with SVD (star-volume distribution) method in QUANT3D (Ryan & Ketcham, 2002). Because volume of interest (VOI) size and location can affect trabecular variables (Kivell et al. 2011; Lazenby et al., 2011), the maximum amount of trabecular bone in the distal and proximal locations of the phalanges and metacarpal heads was examined. The maximum VOI was limited by the number of image slices that can be obtained for the proximodistal depth without encompassing cortical bone at the articular surfaces and empty space in the shaft. This area encompassed a large portion of trabecular bone in all selected areas for all taxa

except for the middle phalanges of some male gorillas. Because these elements are very wide and flat, three smaller trabecular cubes could be extracted. No significant differences in trabecular features were seen in the lateral, medial and centered cube so values for the centered cube were selected for analysis. A best fit sphere VOI for each cube was fitted using Quant 3D and the orientation parameters set to a uniform setting with 513 orientations, random rotation, and dense vectors as recommended by Ketcham and Ryan (2004).

Quant3D generates the following SVD variables: DA (degree of anisotropy), I (isotropy index), E (elongation index), and BV/TV (volume of trabecular bone to total volume). DA, I, and E are calculated from three eigenvalues (ev_{1-3}) generated by Quant3D: $DA = ev_1 / ev_3$; $I = ev_3 / ev_1$; $E = 1 - (ev_1 / ev_3)$). The program also produces three eigenvectors which determine trabecular orientation. The elongation and Isotropy indices when considered together characterize the fabric structure in a given VOI. The three eigenvalues derived from a fabric tensor are used to determine fabric shape. There is a range of fabric shapes between the three end forms: spheres, discs, and rods. Spherical trabeculae are isotropic fabrics with approximately equal eigenvalues ($ev_1 \approx ev_2 \approx ev_3$). Disc-like trabeculae are flattened and plate-like and have approximately equal first and second eigenvalues ($ev_1 \approx ev_2 > ev_3$). Rod-like trabeculae are more linear in form and the second and third eigenvalues are approximately equal ($ev_1 > ev_2 \approx ev_3$) (Ryan and Ketcham, 2002). Trabecular orientation and fabric shape were numerically coded for each location (*orientation*: 1 = medial-lateral or towards digits 2 and 4; 2 = palmar-dorsal; 3 = proximodistal; *fabric shape*: 1 = spherical; 2 = disc-like; 3 = rod-like).

For trabecular orientation the "main" direction of alignment was chosen (i.e. in some cases trabecular bone was aligned in an angular direction along a proximodistal and palmar-dorsal direction and in these cases the "stronger" directionality was chosen and coded). These coded variables, along with DA, I, E, and BV/TV were compared between sexes for each genus using t-tests, and across taxa using the Mann-Whitney U test in SPSS v20. Trabecular orientation and shape for each anatomical location were compared across locomotor categories using chi-square analyses. Paired t-tests were also used to compare orientation and shape of the proximal to the distal locations of the phalanges for each taxon to assess "within element" structural differences.

To assess the discriminating power of a single area of bone, a particular element, and a combination of manual locations, I used several Discriminant Function Analyses (DFA). All DFAs compared locomotor categories for the following variables: DA, I, E, BV/TV, orientation, and shape. Five DFAs were run comparing variables of each anatomical location (i.e. all the variables of the proximal end of the proximal phalanges were included in one DFA). Two DFAs included variables of a single element: one for the proximal and distal ends of the proximal phalanges and one for the proximal and distal ends of the middle phalanges. Finally, I used DFA to compare all variables at all locations across taxa.

Results

The main direction of orientation was determined for each location based on the first SVD eigenvector values. Results are presented in Table 4.2, and compared with

expected orientations in Table 4.3. Orangutans are characterized by more proximodistal alignment in all locations. Macaques have more palmar-dorsal alignment in the proximal ends of the phalanges and more proximodistal alignment in the distal ends and metacarpal heads. In contrast, knuckle walkers and gibbons have more proximodistal alignment in the proximal ends of the phalanges and more palmar-dorsal in the distal ends. Knuckle walkers and gibbons differ in the orientation of the metacarpal trabecular bone: knuckle walkers are more palmar-dorsally aligned and gibbons more proximodistally aligned.

Differences between the Sexes

T-tests reveal no significant differences in the trabecular orientation and trabecular fabric shape between the sexes at any location (proximal and distal ends of the phalanges and the metacarpal head) for any taxon. There were also no differences between the sexes for DA, I, E and BV/TV in the gibbon or orangutan samples. Significant differences were seen between male and female chimpanzees in the trabecular variables of the middle phalanges: males have a greater degree of anisotropy in the proximal ($t = 3.93$, $df = 6$; $P = 0.01$) and distal ends ($t = 3.13$, $df = 6$, $P = 0.04$) of the middle phalanges and females have significantly greater I values at both locations (proximal end $t = -3.5$, $df = 6$, $P = 0.03$; distal end $t = -3.2$, $df = 6$, $P = 0.02$). Female chimpanzees also show increased BV/TV in the proximal ends of the middle phalanges ($t = -5.5$, $df = 6$, $P = 0.008$) and proximal phalanges ($t = -5.8$, $df = 6$, $P = 0.001$). Gorilla males and females differ only in BV/TV for the proximal end of the middle and proximal phalanges: females have increased BV/TV at both locations (middle phalanges $t = -2.5$,

df = 8, P = 0.046; proximal phalanges t = -2.96, df = 8, P =0.018). Subsequent analyses were conducted on pooled male and female samples.

Differences across Taxa and Locomotor Categories

Taken alone, variables (DA, I, E, and BV/TV) show no discernable pattern of differences across taxa that can be related to function or phylogenetic relationships (Table 4). Orientation does show significant differences among taxa attributed to different locomotor categories in several regions. Chimpanzees and gorillas differ significantly from orangutans, and gibbons in trabecular bone orientation of the metacarpal head. Macaques differ significantly in trabecular orientation from the apes in regions of the phalanges. A similar result is seen when the taxa are lumped into locomotor categories (Table 4.5). As there were no significant differences in DA, I, trabecular orientation or shape for orangutans (quadrumanous climbers) and gibbons (brachiators), they were both included in a broader "suspensory" category for this comparison. Quadrupeds differ from suspensory primates in the orientation of trabecular bone in the proximal ends of both phalanges. Knuckle walkers show significant differences from quadrupeds in trabecular orientation at the distal end of the middle phalanges and proximal end of the proximal phalanges, and they are highly significantly different from suspensory primates in trabecular orientation of the metacarpal head.

Chi-square analyses comparing trabecular orientation between the locomotor categories revealed significant differences in several locations. Trabecular orientation was significantly different in the proximal end of the middle phalanges ($X^2 = 0.009$), the

proximal end of the proximal phalanges ($X^2 = 0.001$), and the metacarpal head ($X^2 = 0.002$). In the proximal end of the middle and proximal phalanges, knuckle walkers and suspensory primates have a greater proportion of individuals with a proximodistal alignment (knuckle walkers - 89% in both locations; Suspensory – 92% of middle and 83% of proximal phalanges). Quadrupeds have a greater proportion of palmar-dorsal alignments in both areas (67% in both locations) (Figure 4.1). In contrast to the structure of the phalanges, knuckle walkers have a greater proportion of palmar-dorsal orientation (73%) in the metacarpal head. Suspensory primates have 100% of individuals with a proximodistal alignment in this area, and quadrupeds display nearly equal amounts of proximodistal (60%) and palmar-dorsal (40%) orientations (Figure 4.2).

Theses same areas (proximal ends of the middle and proximal phalanges and metacarpal head) also show significant differences in trabecular bone shape. In the proximal end of the middle phalanges ($X^2 = 0.028$), knuckle walkers have a greater proportion of individuals with "rod-like" trabeculae (72%) and lesser number with more disc-like (28%). Suspensory primates also have a greater proportion of individuals with rod-like trabeculae (93%) and quadrupeds have an equal percentage of "spherical", rod-like, and disc-like trabeculae. A similar pattern is seen in the proximal end of the proximal phalanges ($X^2 = 0.019$) for the knuckle walkers and suspensory primates: both have a greater proportion of individuals with rod-like trabeculae (knuckle walkers = 72%; suspensory = 83%). Quadrupeds have 83% of individuals with disc-like trabeculae. Differences in the metacarpal head approach significance ($X^2 = 0.059$). In this region knuckle walkers and quadrupeds have disc-like trabeculae (knuckle walkers = 73%;

quadrupeds = 100%), and suspensory primates show nearly even proportions of "spherical" (31%), rod-like (38%), and disc-like (31%) trabeculae.

Paired t-tests revealed significant differences between the proximal and distal ends of the phalanges for two taxa. Gorillas have significantly different trabecular orientation at the proximal and distal ends of both phalanges (middle phalanges: $t = 4.6$, $df = 9$, $P < 0.001$; proximal phalanges: $t = 9$, $df = 9$, $P < 0.001$). Gibbons showed significant differences in both shape and orientation. They differ significantly in orientation between the proximal and distal ends of both phalanges (middle phalanges: $t = 3.3$, $df = 6$, $P = 0.017$; proximal phalanges: $t = 3.9$, $df = 6$, $P = 0.008$) and in shape in the proximal and distal ends of the proximal phalanges ($t = 6$, $df = 6$, $P = 0.001$). Both gorillas and gibbons are characterized by a proximodistal alignment at the proximal ends of the phalanges and a more palmar-dorsal alignment at the distal ends.

Discriminant Function Analyses

Middle Phalanges

The Discriminant function analyses for specific locations were successful at discriminating between locomotor categories. The functions for the *proximal* end of the middle phalanges were significant ($X^2 = 30.5$, $df = 12$, $P = 0.002$). This DFA successfully classified 74.3% of original grouped cases. Function 1 accounts for 81% of the variance and polarizes macaques with lower orientation and shape values (more palmar-dorsal, medial-lateral orientation and more spherical and disc-shaped trabeculae) from knuckle walkers and suspensory primates (more proximodistal orientation). Function 2 polarizes knuckle walkers who have higher DA, and less BV/TV than

suspensory primates. The functions for the DFA of the *distal* end of the middle phalanges were not significant. However this analysis correctly classified 71.4% of the original groups. Quadrupeds and suspensory primates with higher E and orientation values are distinguished from knuckle walkers along function 1 (which accounts for 51.8% of variance). Function 2 (48.2% of the variance) differentiates between the three groups with quadrupeds having the highest BV/TV and orientation values and suspensory primates (with the lowest values for BV/TV and orientation). Knuckle walkers fall in the middle. The DFA using variables for both the *proximal* and *distal* ends of the middle phalanges was successful at classifying 85.7% of original grouped cases. The functions were highly significant ($X^2 = 42.2$, df = 24, P = 0.012) and functions 1 and 2 accounted for 62.9% and 37.1% of the variance respectively. All three categories are separated along Function 1 with suspensory primates having the greatest *proximal* end shape and orientation values (more rod-like and proximodistal alignment), knuckle walkers in the middle and quadrupeds the lowest values. Function 2 separates the knuckle walkers with more proximodistal alignment of the *distal* region and less BV/TV from both the quadrupeds and suspensory primates.

Proximal Phalanges

The DFA functions for the *proximal* end of the proximal phalanges is highly significant ($X^2 = 56.3$, df = 12, $P < 0.001$) and correctly classified 82.9% of the originally grouped cases. Function 1 accounts for 81.9% of the variance and separates the quadrupeds with lower BV/TV and orientation values (more palmar-dorsal alignment) from the knuckle walkers and suspensory primates (proximodistal alignment). Function 2 separates the suspensory primates with higher I values and lower DA from both

knuckle walkers and quadrupeds. The DFA functions for the *distal* end of the proximal phalanges were not significant. The DFA correctly classified 62.9% of original groups. Most of the variance is accounted for by function 1 (87.3%) and delineates between all three groups: knuckle walkers have greater I, BV/TV, and orientation values (more proximo-distal alignment) than quadrupeds with the lowest and suspensory primates in the middle. Function 2 weakly separates knuckle walkers and quadrupeds (with higher DA) from suspensory primates. The classification success increases to 85.7% when the DFA is run with variables from both the *proximal* and *distal* ends. The functions were highly significant ($X^2 = 58.4$, df = 24, $P < 0.001$), and most of the variance is accounted for by function 1 (80.7%). This function delineates between all three groups with knuckle walkers having the greatest BV/TV and orientation values (more proximo-distal alignment) in the *proximal* end, macaques the lowest and suspensory primates in the middle. Function 2 separates out the suspensory primates with higher *proximal* end I values and lower *proximal* end DA from the knuckle walkers and quadrupeds.

Metacarpal head

The DFA for the metacarpal head variables correctly classified 93.5% of the original grouped cases. The functions were highly significant ($X^2 = 53.9$, df = 12, $P < 0.001$), and Function 1 accounts for 70.2% of the variance and function 2 for 29.8%. Function 1 differentiates between all three categories with knuckle walkers having the highest BV/TV and lowest orientation values (more palmar-dorsal alignment), quadrupeds the lowest BV/TV and higher orientation values and suspensory primates in the middle (both have more proximodistal alignment). Function 2 separates the

suspensory primates from the knuckle walkers and quadrupeds. The suspensory primates have higher E and shape values (more rod- and disc-like), and higher orientation values (proximodistal alignment).

All Locations

The last DFA was run with the variables (DA, I, E, BV/TV, shape and orientation) for all 5 locations (proximal and distal ends of both phalanges and the metacarpal head). The functions were highly significant ($X^2 = 145.1$, df = 56, $P > 0.001$) and 100% of original cases were correctly classified. Cross validation results show only a correct classification of 48.5% of cases. Function 1 accounts for 91.1% of the variance and delineates between all three locomotor categories: knuckle walkers are characterized by high BV/TV in the proximal and distal ends of the proximal phalanges and proximal end of the middle phalanges and lower orientation values in the metacarpal head and distal end of the proximal phalanges (more palmar-dorsal alignment). Quadrupeds have the lowest BV/TV values and higher orientation values in the aforementioned areas, and suspensory primates fall in between quadrupeds and knuckle walkers (closer to the quadrupeds) (Figure 3). Function 2 differentiates between suspensory primates and the other locomotor categories. Suspensory primates have the higher metacarpal shape and orientation values ("rod-like" in a proximo-distal alignment) and higher orientation values for the proximal end of the middle phalanges.

When the analysis is run with I and E removed to eliminate some variable redundancy (I = inverse of DA, E = 1- DA) the functions remain highly significant ($X^2 = 82.7$, df = 40, $P < 0.001$), 100% of the original cases are correctly classified, and cross validation increases to 64.5% correct classification. The discriminatory factors remain

the same on functions 1 and 2 as in the above analysis (function 1 - 82.4% of variance; function 2 – 17.6%).

Discussion

Trabecular orientation within the manus is sensitive to locomotor function. Taxa assigned to the same locomotor categories have similar trabecular orientation. The latter can be related to the stresses placed on the digits during locomotion. Macaques show a pattern of curvature within the phalanges that somewhat fits the predicted expectation of greater proximodistal alignment in the curved middle phalanges and more palmar-dorsal alignment in the "flatter" proximal phalanges. They do possess increased proximodistal alignment in the distal end of the middle phalanges but all other areas show a greater percentage of palmar-dorsal alignment.

The highly suspensory orangutans, as predicted, had more proximodistal alignment of the trabecular bone at all locations examined. In addition to the extremely high curvature values of these animals, a more proximodistal alignment of the trabecular bone may help to buffer against tensile forces during suspension. The gibbons, although not significantly different from orangutans in orientation at any location, do show some differences from them in distal ends of the phalanges. It was predicted that these agile, brachiators would also have a more proximodistal alignment of trabecular bone in all examined areas to mitigate against tensile strain. In the proximal ends of the phalanges and in the metacarpal head, this prediction holds true, but in the distal ends of the proximal and middle phalanges, there is a greater percentage of individuals with a more

palmar-dorsal alignment. Richmond (2007) has demonstrated using FEA that there is compressive strain dorsally on the proximal phalanges when loaded as in suspension. It is possible that more compressive forces are acting on these areas due to gravitational pull during suspension.

Knuckle walkers show a similar pattern to gibbons in the orientation of trabecular bone in the phalanges. It was predicted that palmar-dorsal alignment would be present in both the proximal and distal ends of the middle phalanges due to the high compressive forces that knuckle walking places upon these elements. However, like the gibbons, knuckle walkers have a more palmar-dorsal alignment in the distal ends of both phalanges and a more proximodistal alignment in the proximal ends. Pressure outputs show increased pressure application in the proximal and distal regions of the middle phalanges (Matarazzo, chapter 2) so it is unclear why a more proximodistal alignment is shown in the proximal end of this element. Strain gage analyses of the phalanges have not been conducted so it cannot be determined for sure what level and direction of strain is being placed upon the phalanges during knuckle walking and suspension. It may be that the proximal ends of the phalanges are experiencing increased tensile forces during suspension. Both chimpanzees and gorillas have a palmar-dorsal orientation of trabecular bone in the metacarpal head. Results obtained for this region coincide with earlier studies (Zeininger et al. 2011) that show more activity in the palmar and dorsal regions of the metacarpal head. This orientation could mitigate strain caused via hyperextension at the metacarpophalangeal joint during knuckle walking.

Although several of the trabecular variables (DA, I, E, BV/TV) taken alone show no pattern that can be related to locomotor function, orientation and shape have proven to differentiate successfully at several locations in the manus. Shape and orientation of the *metacarpal heads* and the *proximal ends* of the phalanges discriminate between locomotor categories. Knuckle walkers and suspensory primates are characterized by having greater proximodistal alignment and rod-like trabeculae in the proximal ends of the phalanges, whereas quadrupeds have a more palmar-dorsal alignment and a variety of trabecular forms. The metacarpal head shows distinct differences between the groups: knuckle walkers have a palmar-dorsal alignment and disc-like trabecular shape, suspensory taxa have a proximodistal alignment and rod-like shape and quadrupeds have a proximodistal alignment and disc-like shape. Again, these two variables, taken alone are successful differentiating among primates practicing different methods of locomotion.

The additional variables (DA, I, E, and BV/TV) discriminate among taxa if coupled with shape and orientation. Using DFA, each location within the manus had greater than 60% accuracy in classifying individuals into three locomotor groups (knuckle walking, quadrupedal, or suspensory). Accuracy increased when regions of the same element were examined together, and reached 100% when variables of all five regions were examined. This is an extremely attractive tool to discern possible locomotor functions within extinct primates as it can be used on a fragmentary element.

Conclusions

Trabecular orientation and fabric shape show distinct differences among primates practicing different modes of locomotion in three areas of the manus (metacarpal head

and proximal ends of both the proximal and middle phalanges). In addition, when a suite of trabecular variables (DA, I, E, BV/TV, shape and orientation) are considered as a unit, the correct classification of a primate into their locomotor category is successful at all examined zones. Knuckle walkers have a distinct pattern of alignment and trabecular fabric shape in the metacarpal head that distinguish them from suspensory and quadrupedal primates. Being able to use isolated zones to predict locomotor propensity is an attractive tool given the fragmentary nature of the fossil record. These manual differences in trabecular structure can be related to locomotor use. Micro CT scans of the manus can help to determine patterns of locomotion in extinct hominoids in a non-destructive manner and may provide insight into the origins of knuckle walking in the hominin lineage.

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Table 4.1: Included samples in trabecular bone analyses.

Taxa	Males	Females	Locomotor category
Pan troglodytes	4	4	Knuckle walking
Gorilla gorilla	5	5	Knuckle walking
Hylobates lar	5	2	Brachiator/Suspensory
Pongo pygmaeus	1	4	Quadrumanus/suspensory
Macaca fascicularis	5		Quadruped

Table 4.2: Percentage of individuals for trabecular orientation in examined regions by genus.

Genus	MDprox	MDdis	PXprox	PXdis	MC head
Pan	**75% prox-dis** 12.5% palm-dor 12.5% med-lat	12% prox-dis **88% palm-dor**	**75% prox-dis** 12.5% palm-dor 12.5% med-lat	25% prox-dis **50% palm-dor** 25% med-lat	17% prox-dis **66% palm-dor** 17% med-lat
Gorilla	**100% prox-dis**	30% prox-dis **70% palm-dor**	**100% prox-dis**	**80% palm-dor** 20% med-lat	22% prox-dis **78% palm-dor**
Pongo	**100% prox-dis**	**80% prox-dis** 20% palm-dor	**100% prox-dis**	**80% prox-dis** 20% med-lat	**100% prox-dis**
Hylobates	**86% prox-dis** 14% palm-dor	14% prox-dis **72% palm-dor** 14% med-lat	**72% prox-dis** 28% palm-dor	14% prox-dis **72% palm-dor** 14% med-lat	**100% prox-dis**
Macaca	33% prox-dis **67% palm-dor**	**83% prox-dis** 17% palm-dor	**80% palm-dor** 20% med-lat	**40% prox-dis** **40% palm-dor** 20% med-lat	**60% prox-dis** 40% palm-dor

MD = middle phalanx, PX = proximal phalanx, MC = Metacarpal, "dis" = distal end, "prox" = proximal end, prox-dis = proximodistal orientation, palm-dor = palmar-dorsal orientation, med-lat = medial lateral orientation. Greater percentages in bold.

Table 4.3: Hypothesized (expected) and observed primary trabecular orientation for taxa.

Locomotor Category	**Include Genus/Genera**	**Expected Trabecular Orientation**	**Primary Observed Orientation**
Knuckle walking	Pan and Gorilla	MD - palmar-dor PX- prox-dis MC - palmar-dor	MDprox – prox-dist MDdis – palmar-dor PXprox – prox-dist PXdis – palmar-dor MC – palmar-dor
Quadrupedal	Macaca	MD- Prox-dis PX- Palm-dor MC Palm-dor	MDprox – palmar-dor MDdis – prox-dis PXprox – palmar-dor PXdis – prox-dis & palmar-dor MC – prox-dis
Suspensory	Hylobates and Pongo	MD- Prox-dis PX- Palm-dor MC- Palm-dor	MDprox - prox-dis MDdis – prox-dis & palmar-dor PXprox- prox-dis PXdis – prox-dis & palmar-dor MC – prox-dis

MD = middle phalanx, PX = proximal phalanx, MC = Metacarpal, “dis” = distal end, “prox” = proximal end, prox-dis = proximodistal orientation, palm-dor = palmar-dorsal orientation, med-lat = medial lateral orientation.

Table 4.4: Mann-Whitney U test results for taxa comparisons. Significance values in parentheses.

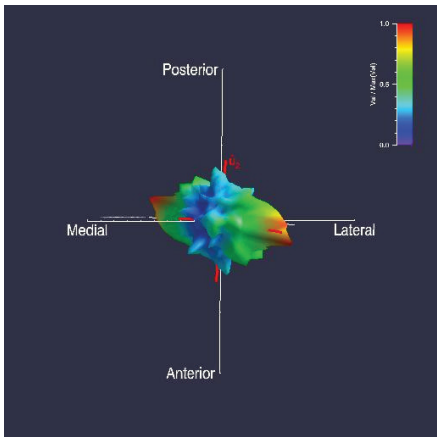
Genus	*Gorilla*	*Pongo*	*Hylobates*	*Macaca*
Pan	**MDdis:** BV/TV(0.03) **PXprox:** DA(0.02), I(0.02), BV/TV(0.03) **MC:** DA(0.01), I(0.01)	**MDdis:** orientation (0.045) **PXprox:** BV/TV(0.01) **MC:** orientation (0.02)	**MDdis:** BV/TV(0.01) **MC:** orientation (0.015)	**MDprox:** shape(0.02) **MDdis:** orientation (0.045) **PXprox:** BV/TV(0.01), orientation(0.045) **MC:** BV/TV(0.004)
Gorilla		**MDprox:** E(0.01), BV/TV(0.04) **MC:** DA(0.01), I(0.01), orientation(0.019)	**PXprox:** orientation(0.01), DA(0.01), I(0.01) **MC:** DA(0.05), orientation(0.01 2)	**MDprox:** orientation (0.013) **PXprox:** E(0.03), BV/TV(0.01), orientation(0.001) **MC:** DA(0.03), I(0.03), BV/TV(0.02)
Pongo			**MDprox:** E(0.03) **PXdis:** BV/TV (0.05)	**MDprox:** E(0.02), shape(0.03), orientation(0.03) **PXprox:** orientation(0.008) **MC**: DA(0.01), I(0.01), BV/TV(0.01)
Hylobates				**MDprox:** shape(0.05) **MDdis:** BV/TV(0.05), orientation(0.048) **PXprox**: DA(0.03), I(0.03), BV/TV(0.01), orientation(0.03) **MC:** BV/TV(0.004)

MD = middle phalanx, PX = proximal phalanx, MC = Metacarpal, “dis” = distal end, “prox” = proximal end

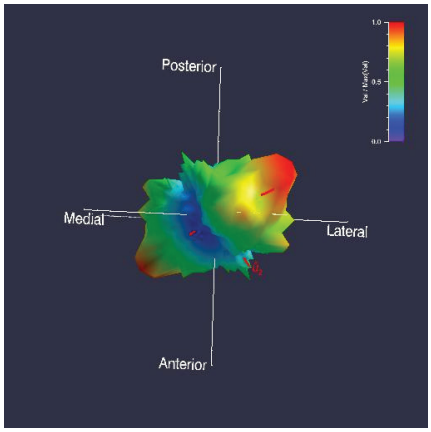
Table 4.5: Mann-Whitney U test results for locomotor category comparisons. Significance values in parenthesis.

Locomotor Categories	Suspensory primates	Quadrupeds
Knuckle walkers	**MDprox:** BV/TV(0.04) **PXprox:** BV/TV(0.05) **MC:** E(0.03), orientation(0.001)	**MDdist:** E(0.03), orientation(0.027) **PXprox:** E(0.01), BV/TV(0.001), orientation(0.002) **PXdist:** DA(0.02), I(0.02) **MC:** BV/TV(0.01)
Suspensory primates		**MDprox:** shape(0.04), orientation(0.05) **PXprox:** shape(0.04), BV/TV(0.01), orientation(0.002) **MC:** BV/TV(0.002)

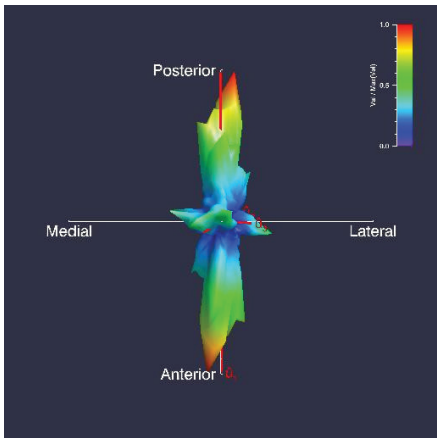
MD = middle phalanx, PX = proximal phalanx, MC = Metacarpal, "dis" = distal end, "prox" = proximal end



A) Knuckle walker



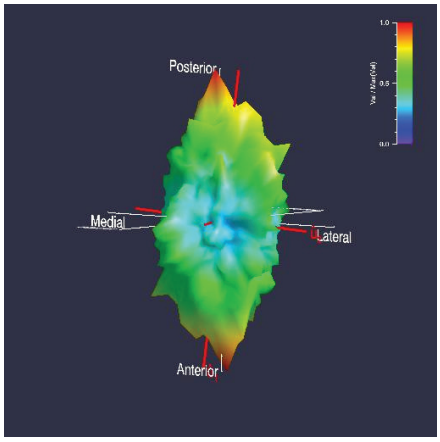
B) Suspensory Primate



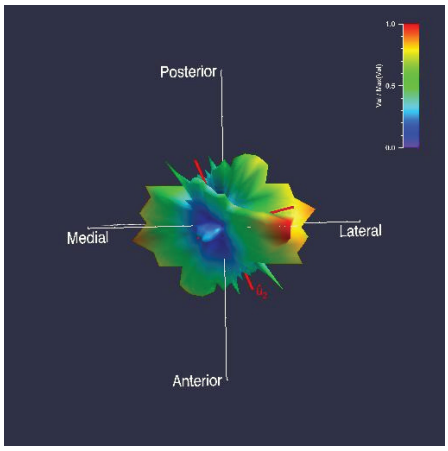
C) Quadruped

Figure 4.1: SVD Rose diagrams displaying the trabecular orientation for the proximal end of the middle phalanx.

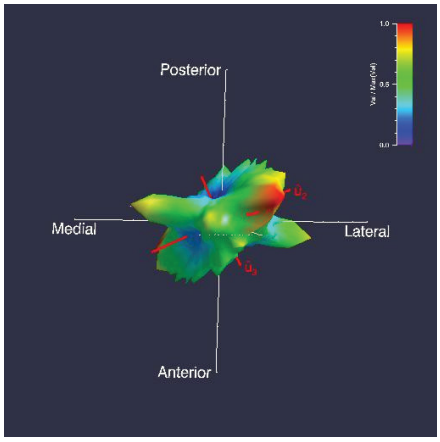
A) Knuckle walker (female gorilla) and B) suspensory primate (female orangutan) main direction of trabecular orientation is towards reader (red area) in a proximo-distal alignment. C) Quadruped (male macaque) has a palmar-dorsal orientation. (Posterior-anterior = palmar-dorsal; proximal-distal runs towards-away from viewer)



A) Knuckle walker



B) Suspensory Primate



C) Quadruped

Figure 4.2: SVD Rose diagrams displaying the trabecular orientation for the metacarpal head.

A) Knuckle walker (female chimpanzee) has a palmar-dorsal trabecular orientation. B) Suspensory primate (male gibbon) and C) quadruped (male macaque) have a proximal-dorsal orientation.

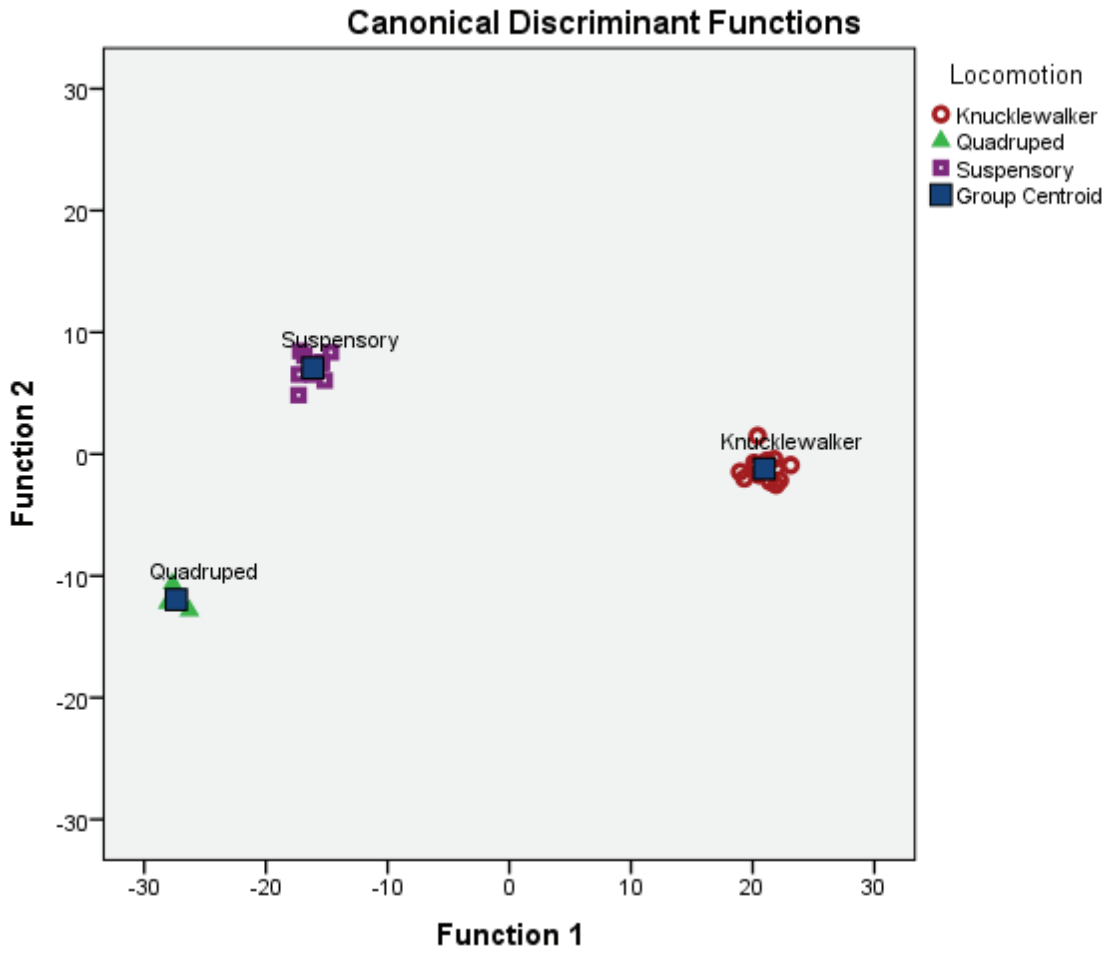


Figure 4.3: Discriminant Function Plot for all included regions (proximal and distal ends of the middle and proximal phalanges and the metacarpal head). Along Function 1, knuckle walkers have high BV/TV in the proximal and distal ends of the proximal phalanges and proximal end of the middle phalanges and more palmar-dorsal alignment in the metacarpal head and distal end of the proximal phalanges. Quadrupeds and suspensory primates have more proximo-distal alignment in those regions.

CHAPTER 5

CONCLUSIONS: KNUCKLE-WALKING SIGNAL IN THE AFRICAN APES AND THE KNUCKLE-WALKING HOMININ HYPOTHESIS

Chapter Summaries

The main goal of this research was to determine whether there is a knuckle-walking signal within manual elements that can be used in paleontological investigations of fossils. To interpret skeletal signals of knuckle walking, it is important to understand how chimpanzees and gorillas actually use their hands in knuckle walking. Therefore, I began with an examination of the pressures applied to the primary weight bearing elements of extant knuckle walkers: the manual middle phalanges. This research resulted in a significant expansion of knuckle walking pressure data collected for chimpanzees and the first pressure data collected for gorillas. I found support for inferences drawn from previous behavioral and kinematic research (Inouye 1994; Tuttle 1967): namely, knuckle-walking chimpanzees use more variable hand positions than do knuckle-walking gorillas. Chimpanzees use both the palm-back and palm-in hand position with approximately equal frequency and touch-off occurs with digits 2 or 3 in the palm-in position and mainly digit 3 in the palm-back position. In contrast, gorillas use the palm-back position almost exclusively and touch-off occurs at either digit 2 or 3. Touch-off digit preference appears related to digit placement in relation to the direction of movement. The third digit of chimpanzees is markedly longer than the other rays and this element is placed forward when the hand is in the palm-back position, making it the final touch-off element. Pressure is highest on the touch-off digit for both taxa. Gorillas have a more even alignment of the knuckle-walking platform and they distribute weight

more evenly across the manus. While these differences may superficially appear to imply different knuckle-walking mechanisms in the two species, it is more accurate to describe gorillas as practicing a smaller subset of the variety of knuckle-walking positions used by chimpanzees.

I documented a number of behavioral and morphological similarities between chimpanzees and gorillas (Table 5.1) – features that distinguish these taxa from other primates. For both chimpanzees and gorillas, pressure application is lightest on the fifth digit. When phalangeal curvature is examined across the manus in knuckle walkers, it is the middle phalanges of digit 5 that have greatest curvature values. The other digits receive relatively greater compressive forces which are reflected in their "flatter" middle phalangeal morphology. The knuckle walkers also have the same profile of middle phalangeal curvature across the manus: digit 5 > digit 2 > digit 3 > digit 4. None of the other taxa (orangutans, gibbons, spider monkeys, capuchins, macaques) whose phalangeal curvature was measured for all four digits exhibit the same curvature profile. The other apes included in the analyses (orangutans and gibbons) are both highly suspensory, but each differs in curvature profile from each other and from the closely related knuckle walkers (orangutans: digit 3 > digit 4 > digit 2 > digit 5; gibbons: digit 4 > digit 3 > digit 5 > digit 2).

Knuckle walkers also share similar Indices of Relative Curvature (middle phalangeal curvature/proximal phalangeal curvature) in digits 2-5. Their middle phalanges are relatively flatter than their proximal phalanges giving them indices that are

less than one (~.85) for each digit 2-5. This distinguishes them from taxa practicing other modes of locomotion. Capuchins and macaques are separated by phylogenetic distance but both practice similar forms of quadrupedalism and share indices of relative curvature that are greater than one on all digits 2-5. These indices reflect greater curvature in the middle phalanges than in the proximal. The gibbons and spider monkeys, separated by the same phylogenetic distance, both practice a fast, fluid brachiation and share similar indices of relative curvature that approximately equal one in each digit 2-5. Only orangutans fail to differentiate from knuckle walkers based on indices alone. In this case the quadrumanous climbers also have indices that are less than one, but this is not reflective of middle phalanges that are "flat". Orangutans have extremely high proximal phalangeal curvature values and high middle phalangeal curvature values that are greater than any other extant primate (Matarazzo, 2008). The locomotor signal originally seen in digit 3 (Matarazzo, 2008) is also seen in digits 2 and 4, and 5, and each of these rays can be used to discriminate among knuckle walkers, brachiators, quadrupeds, and quadrumanous climbers. When indices are derived from measurements of phalanges from different rays within the same manus, they still are able to differentiate between locomotor categories. Bootstrapping analysis also shows that the locomotor signal is present even if indices are derived from measurements of middle and proximal phalanges from different individuals of the same species. This increases the applicability of this locomotor signal to the fossil record, given that elements of the same ray are rarely recovered.

The trabecular bone structure of the phalanges and metacarpal head also show differences among locomotor categories. Trabecular bone orientation in the proximal ends of both the middle and proximal phalanges and in the metacarpal head showed significant differences among knuckle walkers, quadrupeds, and suspensory primates (brachiators and quadrumanous climbers). The proximal ends of the proximal and middle phalanges have trabecular bone aligned in a proximodistal direction in knuckle walkers and suspensory taxa, and palmar-dorsal in the quadrupeds. In the metacarpal head, all knuckle walkers have a palmar-dorsal alignment, most suspensory primates are more proximodistally aligned, and quadrupeds show approximately equal numbers of individuals with either proximodistal or palmar-dorsal orientations. Knuckle-walking taxa are characterized by a pattern of orientation (proximodistal alignment in the proximal ends of the phalanges and palmar-dorsal in the distal ends) that was not predicted based on the known pressure applications. It was originally expected that the middle phalanges would have a palmar-dorsal orientation at both proximal and distal ends due to the compressive forces applied during knuckle walking, and that the curved proximal phalanges would have a proximodistal orientation at both locations. It is possible that the proximal ends of the phalanges are experiencing increased tensile and torsional forces during suspension and this is affecting the trabecular bone orientation in these locations. Quadrupedal primates show an "opposite" pattern of palmar-dorsal alignment in the proximal ends and proximodistal alignment in the distal regions. Suspensory taxa have primarily a proximodistal alignment at all examined locations as predicted based on the high tensile forces that these joints are subjected to during suspension. The ability to differentiate between locomotor categories in all examined

locations was enhanced when a suite of trabecular features were included in analyses (orientation, shape, degree of anisotropy (DA), isotropy index (I), elongation index (E), bone volume (BV/TV)). All individuals were correctly classified in their locomotor groups when all variables for all manual locations were used in discriminant function analysis. The ability to use even one location to derive a possible locomotor pattern is useful if a fossil is too fragmentary to reconstruct to estimate a curvature value (possibly via Deane and Begun's (2008) method of high resolution polynomial curve fitting).

Knuckle-walking Ancestor

Earlier attempts to locate a knuckle-walking signal focused on the wrist and metacarpals of hominins and extant primates (Corruccini and McHenry, 2001; Dainton, 2001; Dainton and Macho, 1999; Inouye and Shea 2004; Kelly, 2001; Richmond and Strait, 2000; Richmond et al., 2001; Shea and Inouye, 1993; Williams 2010). The results of these analyses have been controversial. Although the wrist and metacarpals are held in a distinct manner during knuckle walking (extension at the wrist and metacarpophalangeal joint), no morphological feature has been described for these areas that differentiates knuckle walkers clearly from taxa using other types of locomotion. The primary focus of the wrist has been the examination of possible extension limiting mechanisms of the distal radius (for a review see Richmond et al., 2001). Within the African apes, extension is limited to a relatively large scaphoid notch on the distal radius. Richmond and Strait (2000) argued that this feature can be linked to knuckle walking and is seen in *Australopithecus anamensis* and *A. afarensis*. This claim was contested based on the presence of other "soft-tissue" mechanisms to limit extension and similar

extension limiting factors noted in terrestrial quadrupeds (Lovejoy et al., 2001; Richmond et al., 2001; Tuttle, 1967). A similar problem is noted with the morphology of the metacarpals: many features are not specific to *Pan* and *Gorilla* but rather are often present in terrestrial digitigrade taxa (McCrossin and Benefit, 1997; Richmond et al., 2001; Sarmiento, 1988).

The manual phalanges were largely ignored in this debate. Although it was predicted that the dorsal surface of the middle phalanges of knuckle walkers should be straighter to allow for greater dissipation of weight, examinations of these elements was not undertaken in previous research (Richmond et al., 2001). In fact, Richmond and colleagues (2001) noted their "surprise" that given the role that the proximal and middle phalanges played in knuckle walking "that no clear knuckle-walking adaptations are known in these bones" (p.95). If analysis is limited to the external morphology of either the proximal or middle phalanges, then this statement is somewhat true. However, when curvature values of the elements are compared, or internal trabecular features are examined, a much different outcome applies. There is, indeed, a clear knuckle-walking signal. The indices of relative curvature and trabecular bone features show definitive differences among taxa that are related to locomotor function and not phylogeny. These features can be measured without destruction. Thus they provide excellent tools for determining locomotor patterns from the manual elements of rare fossil hominins to determine a possible locomotor pattern.

As mentioned earlier, chimpanzees are much more variable than gorillas in their hand placement during knuckle walking. They use both palm-in and palm-back hand

positions about equally and individual chimpanzees show more variation with preferred hand position than gorillas. Gorillas are more consistent in their posture, hand use (palm-back) and digit use (2-5). In fact, gorillas are practicing a subset of the various knuckle-walking positions used by chimpanzees. This consistency may be related to the greater reliance on knuckle walking by gorillas, and it is reflected in the digit lengths of these two taxa. Gorillas have relatively even digit lengths providing for a more "stable" knuckle-walking platform, while chimpanzees have proportionally longer digits 3 and 4. These longer rays are related to increased suspensory behaviors in this taxon. Because of the disproportionate lengths, digit 3 is frequently pushed forward of the other rays when chimpanzees use the palm-back hand position. This implies that the difference in touch-off digit by chimpanzees and gorillas is not one of preference but rather it is related to structural differences.

Despite the length pattern differences, chimpanzees and gorillas are the only two taxa to share a phalangeal curvature profile. They have similar indices of relative curvature, and similar trabecular bone features. These morphological features coupled with the similarities noted in their knuckle-walking behavior support a shared origin of knuckle walking (and by implication, a knuckle-walking human ancestor).

Table 5.1: Similarities and Differences between *Pan* and *Gorilla*.

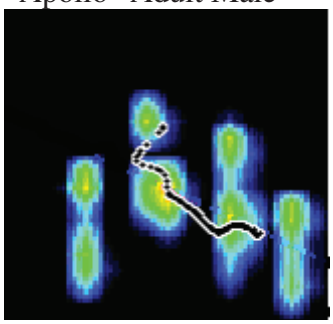
		Similarities	Differences
Pan & *Gorilla*	Pressure	Both use palm-in and Palm-back hand positions.	*Pan* has more variation in hand position use. *Gorilla* use palm-back almost exclusively
		Both touch-down with ulnar aspect of hand.	*Gorilla* has more even pressure distribution across the hand.
		Least amount of pressure on digit 5.	
		Most often touch-off with either digit 2 or 3.	
	Morphology (External)		*Gorilla* has more even digit lengths and more "stable" knuckle-walking platform. *Pan* has disproportionate digit lengths (digits 3 and 4 longer).
		Same pattern of phalangeal curvature across the manus: Px5> Px2> Px4> Px3; and Md5> Md2> Md3> Md4.	
		Similar Indices of Relative Curvature	
	Morphology (Internal)	Palmar-dorsal trabecular bone orientation in the metacarpal head, and distal ends of phalanges.	
		Proximodistal trabecular bone orientation in proximal ends of phalanges.	

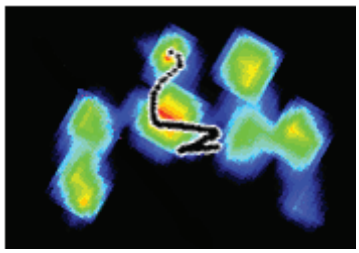
APPENDIX A
MANUAL PRESSURE PRINTS OF KNUCKLE-WALKING APES

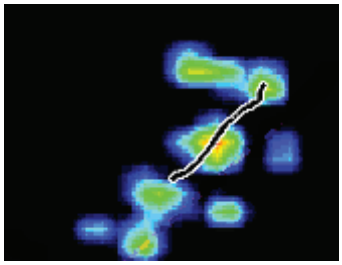
Knuckle-walking pressure print samples from chimpanzees and gorillas. Red color denotes increased pressure point. Black line shows center of pressure movement throughout the step. Images are not to scale. (PI = Palm-in; PB = Palm back; CC# = step code; TO# = Touch-off digit #)

Chimpanzees

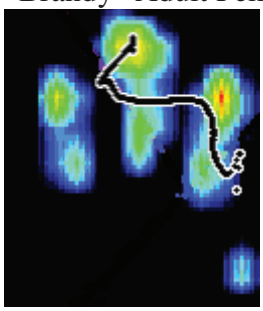
"Apollo" Adult Male

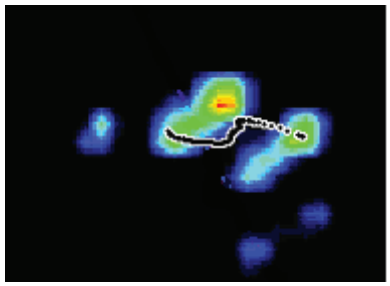

PB Right hand (CC6) TO3

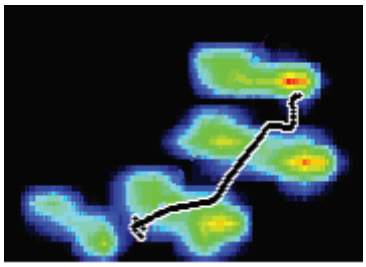

PB Right hand (CC3) TO3


PI Right hand (CC5) TO2

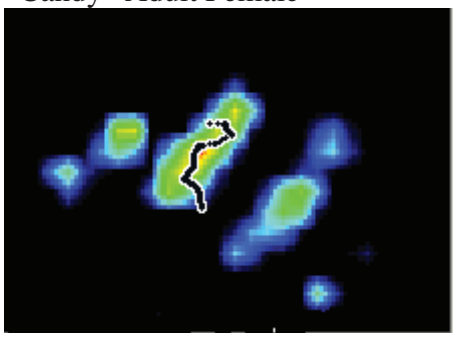
"Brandy" Adult Female

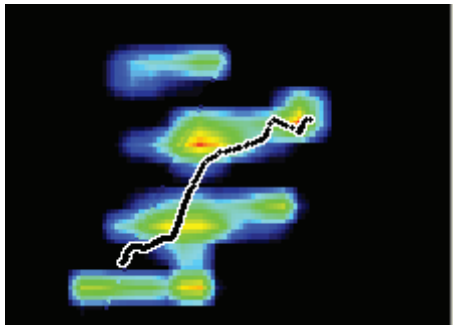

PB Right hand (CC29) TO3


PB Left hand (CC38) TO3


PI Right hand (CC106) TO2

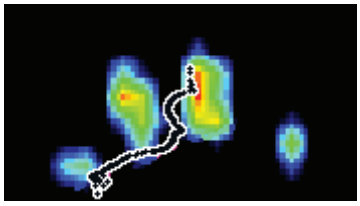
"Candy" Adult Female

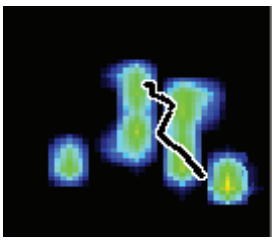

PB Right hand (CC71) TO3

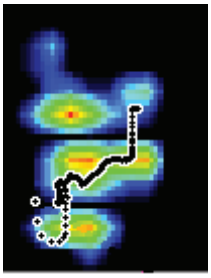

PI Right hand (CC17) TO3

Appendix A continued: Chimpanzees

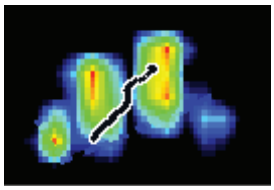
"Zack" Juvenile Male

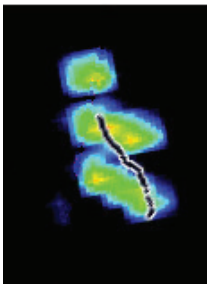

PB Left hand (CC50) TO3


PB Right hand (CC6) TO3


PI Right hand (CC9) TO3

"Manetta" Juvenile Female

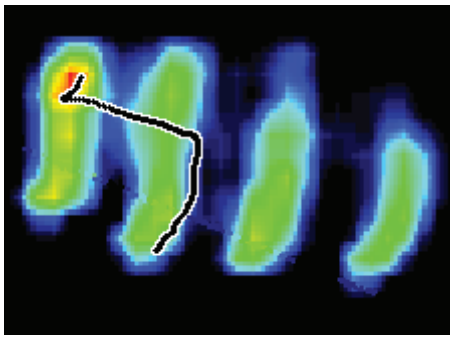

PB Left hand (CC15) TO3


PI Left hand (CC36) TO3

Appendix A continued: Gorillas

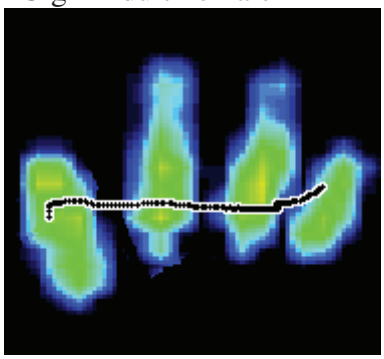
Gorillas

"Kwan" Adult Male:



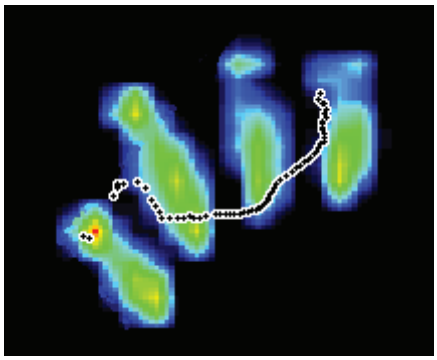
PB Right hand (CC9) TO2

"Gigi" Adult Female

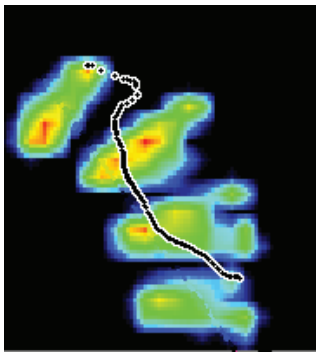


PB Right hand (CC G1) TO2

"Medini" Adult Female



PB Right hand (CC21) TO2



PI Right hand (CC19) TO2

APPENDIX B
INDICES OF RELATIVE CURVATURE BOOTSTRAPPING RESULTS

Results of bootstrapping analyses for Indices of Relative Curvature (Md#/Px#). Means, Standard Deviations (SD), and the Minimum, Maximum and Median indices are presented for the bootstrapped indices (1000 iterations) composed of any individual (male or female) from each taxon.

A. Brachiators

	Ateles spp.				*Hylobates lar*			
Index	Mean(SD)	Min.	Max.	Median	Mean(SD)	Min.	Max.	Median
Md2/Px2	1.04(0.18)	0.72	1.5	0.998	1.09(0.18)	0.66	1.7	1.07
Md3/Px3	0.999(0.18)	0.58	1.4	0.99	1.03(0.17)	0.68	1.6	1.02
Md4/Px4	1.0(0.18)	0.62	1.5	0.98	1.11(0.14)	0.79	1.5	1.11
Md5/Px5	1.12(0.25)	.75	1.9	1.08	1.04(0.18)	0.69	1.7	1.01
Md2/Px3	0.997(0.13)	0.67	1.3	1.01	1.0(0.16)	0.65	1.5	0.996
Md2/Px4	0.999(0.16)	0.67	1.4	0.98	1.03(0.15)	0.68	1.4	1.02
Md2/Px5	1.07(0.2)	0.73	1.6	1.04	1.02(0.19)	0.63	1.7	1.0
Md3/Px2	1.04(0.21)	0.63	1.6	1.01	1.11(0.19)	0.69	1.7	1.1
Md3/Px4	1.0(0.2)	0.59	1.5	0.98	1.05(0.17)	0.72	1.4	1.05
Md3/Px5	1.08(0.24)	0.64	1.8	1.04	1.04(0.2)	0.66	1.7	1.03
Md4/Px2	1.04(0.19)	0.66	1.6	1.0	1.17(0.18)	0.77	1.7	1.15
Md4/Px3	1.0(0.15)	0.61	1.4	1.0	1.08(0.16)	0.75	1.6	1.08
Md4/Px5	1.08(0.22)	0.67	1.8	1.04	1.1(0.19)	0.73	1.7	1.07
Md5/Px2	1.08(0.22)	0.74	1.7	1.06	1.1(0.16)	0.72	1.6	1.1
Md5/Px3	1.04(0.17)	0.69	1.5	1.01	1.02(0.15)	0.71	1.5	1.01
Md5/Px4	1.04(0.2)	0.69	1.5	1.03	1.04(0.13)	0.75	1.4	1.05

B. Quadrupeds

	Sapajus apella				*Macaca* spp.			
Index	Mean (SD)	Min.	Max.	Median	Mean (SD)	Min.	Max.	Median
Md2/Px2	1.28(0.2)	0.8	1.9	1.29	1.13(0.2)	0.73	1.8	1.12
Md3/Px3	1.24(0.21)	0.84	1.9	1.23	1.11(0.19)	0.7	1.8	1.1
Md4/Px4	1.33(0.19)	0.93	1.9	1.32	1.05(0.16)	0.59	1.7	1.05
Md5/Px5	1.28(0.13)	0.96	1.6	1.3	1.18(0.17)	0.76	1.7	1.17
Md2/Px3	1.27(0.21)	0.79	1.8	1.3	1.16(0.2)	0.72	1.8	1.13
Md2/Px4	1.31(0.19)	0.87	1.9	1.31	1.1(0.21)	0.66	2.0	1.08
Md2/Px5	1.2(0.17)	0.76	1.5	1.24	1.14(0.19)	0.73	1.7	1.12
Md3/Px2	1.25(0.21)	0.85	1.9	1.23	1.09(0.2)	0.7	1.7	1.08
Md3/Px4	1.28(0.2)	0.93	1.9	1.26	1.06(0.2)	0.64	1.9	1.05
Md3/Px5	1.17(0.17)	0.81	1.6	1.15	1.1(0.18)	0.71	1.7	1.09
Md4/Px2	1.3(0.21)	0.86	2.0	1.29	1.08(0.16)	0.65	1.5	1.08
Md4/Px3	1.29(0.21)	0.84	1.9	1.28	1.11(0.16)	0.64	1.5	1.09
Md4/Px5	1.22(0.17)	0.81	1.6	1.23	1.09(0.14)	0.66	1.4	1.08
Md5/Px2	1.37(0.18)	1.02	1.9	1.36	1.17(0.19)	0.76	1.8	1.15
Md5/Px3	1.36(0.19)	0.99	1.9	1.36	1.2(0.19)	0.75	1.8	1.18
Md5/Px4	1.4(0.17)	1.1	1.9	1.38	1.14(0.2)	0.69	2.0	1.13

C. Knuckle walkers

	Pan troglodytes				*Gorilla gorilla*			
Index	Mean (SD)	Min.	Max.	Median	Mean (SD)	Min.	Max.	Median
Md2/Px2	0.93(0.15)	0.6	1.6	0.92	0.87(0.13)	0.44	1.5	0.87
Md3/Px3	0.88(0.13)	0.55	1.4	0.86	0.84(0.12)	0.48	1.4	0.83
Md4/Px4	0.86(0.12)	0.57	1.4	0.85	0.81(0.11)	0.5	1.2	0.8
Md5/Px5	0.94(0.13)	0.6	1.4	0.93	0.87(0.12)	0.58	1.5	0.86
Md2/Px3	0.94(0.15)	0.55	1.5	0.93	0.88(0.13)	0.46	1.5	0.88
Md2/Px4	0.93(0.14)	0.58	1.5	0.91	0.88(0.13)	0.47	1.4	0.87
Md2/Px5	0.91(0.14)	0.58	1.4	0.89	0.86(0.13)	0.46	1.5	0.85
Md3/Px2	0.87(0.13)	0.6	1.4	0.86	0.83(0.11)	0.44	1.3	0.82
Md3/Px4	0.87(0.12)	0.58	1.3	0.85	0.83(0.11)	0.49	1.3	0.83
Md3/Px5	0.84(0.12)	0.58	1.3	0.83	0.81(0.11)	0.47	1.4	0.8
Md4/Px2	0.87(0.13)	0.59	1.5	0.85	0.8(0.11)	0.46	1.2	0.79
Md4/Px3	0.87(0.13)	0.54	1.4	0.86	0.81(0.12)	0.48	1.3	0.81
Md4/Px5	0.84(0.12)	0.57	1.4	0.83	0.79(0.11)	0.47	1.2	0.78
Md5/Px2	0.97(0.14)	0.63	1.5	0.96	0.88(0.13)	0.56	1.5	0.87
Md5/Px3	0.98(0.13)	0.58	1.5	0.97	0.9(0.13)	0.58	1.5	0.89
Md5/Px4	0.97(0.13)	0.61	1.4	0.96	0.89(0.12)	0.6	1.4	0.88

D. Quadrumanous climbers

	Pongo pygmaeus			
Index	Mean (SD)	Min.	Max	Median
Md2/Px2	0.91(0.11)	0.63	1.3	0.92
Md3/Px3	0.91(0.1)	0.66	1.2	0.89
Md4/Px4	0.89(0.1)	0.64	1.4	0.89
Md5/Px5	0.88(0.11)	0.56	1.3	0.88
Md2/Px3	0.88(0.1)	0.64	1.2	0.88
Md2/Px4	0.88(0.1)	0.63	1.4	0.88
Md2/Px5	0.91(0.12)	0.6	1.4	0.89
Md3/Px2	0.94(0.11)	0.65	1.3	0.93
Md3/Px4	0.91(0.11)	0.67	1.3	0.9
Md3/Px5	0.93(0.12)	0.64	1.5	0.92
Md4/Px2	0.93(0.11)	0.6	1.3	0.93
Md4/Px3	0.9(0.09)	0.64	1.2	0.89
Md4/Px5	0.92(0.12)	0.61	1.4	0.91
Md5/Px2	0.89(0.1)	0.59	1.2	0.89
Md5/Px3	0.86(0.1)	0.6	1.2	0.86
Md5/Px4	0.86(0.1)	0.57	1.2	0.86

BIBLIOGRAPHY

Barak MM, Lieberman DE, and Hublin JJ. 2011. A Wolff in sheep's clothing: Trabecular bone adaptation in response to changes in joint loading orientation. *Bone* 49(6):1141-1151.

Barden MB, Wunderlich RE, Demes, B. 2010. Plantar pressure during bipedalism and quadrupedalism in *Cebus*. *Am J Phys Anthropol* Suppl. 50:61.

Begun DR. 1993. Response to 'Knuckle-walking ancestors' (Shea and Inouye). *Science* 259:294.

Berillon G, Daver G, D'Aout K, Nicolas G, de la Villetanet B, Multon F, Digrandi G, Dubreuil G. 2010. Bipedal versus quadrupedal hind limb and foot kinematics in a captive sample of *Papio anubis*: setup and preliminary results. *Int J Primatol* 31:159-180.

Bertram JEA. 2004. New perspectives on brachiation mechanics. *Yrbk Phys Anthropol* 47:100-117.

Bertram JEA and Chang Y. 2001. Mechanical energy oscillations of two brachiation gaits: Measurement and Simulation. *Am J Phys Anthropol* 115:319-326.

Bertsch C, Unger H, Winkelmann W, Rosenbaum D. 2004. Evaluation of early walking patterns from plantar pressure distribution measurements. First year results of 42 children. *Gait and Posture* 19:235-242.

Burr DB, Ruff CB and Johnson C.1989. Structural adaptations of the femur and humerus toarboreal and terrestrial environments in three species of macaque. *Am J Phys Anthropol* 79:357-367.

Cant JGH.1988. Positional behavior of long-tailed macaques (*Macaca fascicularis*) in Northern Sumatra. *Am J Phys Anthropol* 76:29-37.

Cant JGH, Youlatos D and Rose MD. 2001. Locomotor behavior of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: general patterns and nonsuspensory modes. *J Hum Evol* 41:141-166.

Cant JGH, Youlatos D, and Rose MD. 2003. Suspensory locomotion of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador. *J Hum Evol* 44:685-699.

Carlson KJ and Patel BA. 2006 Habitual use of the primate forelimb is reflected in the material properties of subchondral bone in the distal radius. *J Anat* 208:659-670.

Cartmill, M. 1985. *Climbing*. In Functional Vertebrate Morphology. (Eds. M Hildebrand, DM Bramble, KF Kiem, & DB Wake) Harvard Univ. Press: Cambridge, MA, pp. 73–88.

Chang Y, Bertram JEA and Lee DV. 2000. External forces and torques generated by the brachiating white-handed gibbon (*Hylobates lar*). *Am J Phys Anthropol* 113:201-216.

Chirchir H, Richmond BG, Griffon NL, Nakatsukasa M, Zeininger A, and Ketcham RA. 2010. Hand biomechanics and trabecular architecture in hominoid metacarpals. *Am J Phys Anthropol* 141(S50):81.

Corruccini RS. 1978. Comparative osteometrics of the hominoid wrist joint, with special reference to knuckle-walking. *J Hum Evol* **7:**307–321.

Corruccini RS and McHenry HM. 2001. Knuckle-walking hominid ancestors. *J Hum Evol* 40:507-511.

D'Aout K, Vereecke E, Schoonaert K, De Clercq D, Van Elsacker L, Aerts P. 2004. Locomotion in bonobos (*Pan paniscus*): differences and similarities between bipedal and quadrupedal terrestrial walking, and a comparison with other locomotor modes. *J Anat* 204:353-361.

Dainton M. 2001. Did our ancestors knuckle-walk? *Nature* 410:324-325.

Dainton M and Macho GA. 1999. Did knuckle walking evolve twice? *J Hum Evol* 36:171-194.

Deane AS and Begun DR. 2008. Broken fingers: retesting locomotor hypotheses for fossil hominoids using fragmentary proximal phalanges and high-resolution polynomial curve fitting (HR-PCF). *J Hum Evol* 55:691-701.

DeSilva JM and Devlin MJ. 2012 A comparative study of the trabecular bony architecture of the talus in humans, non-human primates, and *Australopithecus*. *J Hum Evol* 63:536-551.

Doran DM. 1993. Sex differences in adult chimpanzee positional behavior: The influenceof body size on locomotion and posture. *Am J Phys Anthropol* 91:99-115.

Doran DM.1997. Ontogeny of locomotion in mountain gorillas and chimpanzees. *J Hum Evol* 32:323-344.

Fajardo RJ and Muller R. 2001. Three-dimensional analysis of nonhuman primate trabecular architecture using micro-computed tomography. *Am J Phys Anthropol* 115:327-336.

Fajardo RJ, Ryan TM, and Kappelman J. 2002. Accessing the accuracy of high resolution X-ray computed tomography of primate trabecular bone by comparisons with histological sections. *Am J Phys Anthropol* 118:1-10.

Fox JC and Keaveny TM. 2001. Trabecular Eccentricity and Bone Adaptation. *J Theor Biol* 212:211-221.

Garber PA and Rehg JA. 1999. The ecological role of the prehensile tail in white-faced capuchins (*Cebus capucinus*). *Am J Phys Anthropol* 110:325-339.

Gebo DL. 1996. Climbing, brachiation, and terrestrial quadrupedalism: historical precursors of hominid bipedalism. *Am J Phys Anthropol* 101:55-92.

Hayama S, Chatani K and Nakatsukasa M. 1994. The digitigrade hand and terrestrial adaptation in Japanese macaques. *Anthropol Sci* 102:115-125.

Inouye SE. 1992. Ontogeny and allometry of African ape manual rays. *J Hum Evol* 23:107-138.

Inouye SE. 1994. Ontogeny of knuckle-walking hand postures in African apes. *J Hum Evol* 26:459-485.

Inouye SE and Shea BT. 2004. The implications of variation in knuckle-walking features for models of African hominoid locomotor evolution. *J Anthropol Sci* 82:67-88.

Jacobs CR. 2000. The mechanobiology of cancellous bone structural adaptation. *J Rehab Research Devel* 37(1):209-216.

Jungers WL, Godfrey LR, Simons EL and Chatrath PS. 1997. Phalangeal curvature and positional behavior in extinct sloth lemurs (Primates, Palaeopropithecidae). *Proc Natl Acad Sci* 94:11998-12001.

Jungers WL, Godfrey LR, Simons EL, Wunderlich RE, Richmond BG and Chatrath PS. 2002. *Ecomorphology and behavior of giant extinct lemurs from Madagascar*. In Reconstructing behavior in the primate fossil record. (Eds. JM Plavcan, RF Kay, WL Jungers, & CP van Schaik) Kluwer Academic Press/Plenum Publishers: New York. pp 371-411.

Jungers WL, Simons EL and Godfrey LR. 1994. Phalangeal curvature and locomotor adaptations in subfossil lemurs. *Am J Phys Anthropol* 18:117-118.

Keaveny TM, Morgan EF, Niebur GL, and Yeh OC. 2001. Biomechanics of trabecular bone. *Annu Rev Biomed Eng* 3:307-333.

Kelly RE. 2001. Tripedal knuckle-walking: A proposal for the evolution of human locomotion and handedness. *J Theor Biol* 213:333-358.

Ketcham RA. 2005. Three-dimensional grain fabric measurements using high-resolution X-ray computed tomography. *J Struct Geol* 27:1217-1228.

Ketcham RA and Ryan TM. 2004. Quantification and visualization of anisotropy in trabecular bone. *J Microscopy* 213(2):158-171.

Kivell TL and Schmitt D. 2009. Independent evolution of knuckle-walking in African apes shows that humans did not evolve from a knuckle-walking ancestor. *Proc Nat Acad Sci* 106(34):14241-14246.

Kivell TL, Skinner MM, Lazenby R, and Hublin JJ. 2011. Methodological considerations for analyzing trabecular architecture: an example from the primate hand. *J Anat* 218*:209-*225.

Lazenby RA, Skinner MM, Hublin J, and Boesch C. 2011. Metacarpal Trabecular Architecture Variation in the Chimpanzee (*Pan troglodytes*): Evidence for locomotion and tool-use? *Am J Phys Anthropol* 144:215-225.

Lazenby RA, Skinner, Kivell TL, and Hublin JJ. 2011. Scaling VOI size in 3D μCT studies of trabecular bone: A test of the over-sampling hypothesis. *Am J Phys Anthropol* 144:196-203.

Lovejoy CO, Heiple KG and Meindl RS. 2001. Reply to "Did our ancestors knuckle-walk?" *Nature* 410:325-326.

MacLatchy L and Muller R. 2002. A comparison of the femoral head and neck trabecular architecture of *Galago* and *Perodicticus* using micro-computed tomography (μCT). *J Hum Evol* 43:89-105.

Marchi D. 2005. The cross-sectional geometry of the hand and foot bones of the Hominoidea and its relationship to locomotor behavior. *J Hum Evol* 49:743-761.

Matarazzo SA. 2008 Knuckle walking signal in the manual digits of *Pan* and *Gorilla. Am J Phys Anthropol.* 135:27-33.

McCrossin ML and Benefit BR. 1997. *On the relationships and adaptations of Kenyapithecus, a large-bodied hominoid from the Middle Miocen of Eastern Africa*. In Primate Locomotion: recent advances. (Eds. D Begun, C Ward, & M Rose) Plenum Press: New York. pp 353-396.

Mittra E, Rubin C, and Qin Y. 2005. Interrelationship of trabecular mechanical and microstructural properties in sheep trabecular bone. *J Biomech* 38:1229-1237.

Morton DJ. 1926. Evolution of man's erect posture (preliminary report). *J Morphol* 43(1):147-179.

Patel BA. 2010. Functional morphology of cercopithecoid primate metacarpals. *J Hum Evol* 58:320-337.

Patel BA and Carlson KJ. 2007. Bone density spatial patterns in the distal radius reflect habitual hand postures adopted by quadrupedal primates. *J Hum Evol* 52:130-141.

Patel BA and Wunderlich RE. 2010. Dynamic pressure patterns in the hands of olive baboons (*Papio anubis)* during terrestrial locomotion: implications for cercopithecoid primate hand morphology. *Anatom Record* 293:710-718.

Perelman P, Johnson WE, Roos C, Seuanez HN, Horvath JE, Moreira MA, Kessing B, Pontius J, Scheinder MP, Silva A, O'Brien SJ, and Pecon-Slattery J. 2011. A molecular phylogeny of living primates. *PLOS Genetics* 7(3):e1001342.

Polk JD, Williams SA, Peterson JV, Roseman CC, and Godfrey LR. 2010. Subchondral bone apparent density and locomotor behavior in extant primates and subfossil lemurs *Hadropithecus* and *Pachylemur*. *Int J Primatol* 31:275-299.

Polk JD, Blumenfeld J, and Ahlumwalia D. 2008. Knee posture predicted subchondral apparent density in the distal femur: An experimental validation. *Anatom Record* 291:293-302.

Pontzer H, Lieberman DE, Momin E, Devlin MJ, Polk JD, Hallgrimsson B, and Cooper DM. 2006. Trabecular bone in the bird knee responds with high sensitivity to changes in load orientation. *J Exp Biol* 209:57-65.

Remis MJ. 1998. *The gorilla paradox: the effects of body size and habitat on the positional behavior of lowland and mountain gorillas*. In Primate Locomotion: recent advances. (Eds. D Begun, C Ward, & M Rose) Plenum Press: New York. pp. 353-396.

Richmond BG. 1998. Ontogeny and biomechanics of phalangeal form in primates. Ph.D dissertation, State University of New York at Stony Brook, Stony Brook.

Richmond BG. 2007. Biomechanics of phalangeal curvature. *J Hum Evol* 53:678-690.

Richmond BG, Begun DR and Strait DS. 2001. Origin of human bipedalism: The knucklewalking hypothesis revisited. *Yrbk Phys Anthropol* 44:70-105.

Richmond BG and Strait DS. 2000. Evidence that humans evolved from a knuckle-walking ancestor. *Nature* 404:382-385.

Richmond BG and Strait DS. 2001a. Knuckle-walking hominid ancestor: a reply to Corruccini and McHenry. *J Hum Evol* 40:513-520.

Richmond BG and Strait DS. 2001b. Reply to "Did our ancestors knuckle-walk?" *Nature* 410:326.

Rodman PS. 1979. Skeletal differentiation of *Macaca fascicularis* and *Macaca nemestrina* in relation to arboreal and terrestrial quadrupedalism. *Am J Phys Anthropol* 51:51-62.

Ruff C, Holt B, and Trinkaus E. 2006. Who's Afraid of the Big Bad Wolff?: "Wolff's Law" and Bone Functional Adaptation. *Am J Phys Anthropol* 129:484-498.

Ryan TM and Ketchum RA. 2002. The three-dimensional structure of trabecular bone in the femoral head of strepsirrhine primates. *J Hum Evol* 43:1-26.

Ryan TM and Shaw CN. 2012. Unique suites of trabecular bone features characterize locomotor behavior in human and non-human Anthropoid primates. *PLoS ONE* 7(7):e41037.

Ryan TM and van Rietbergen B. 2005. Mechanical significance of femoral head trabecular bone structure in Loris and Galago evaluated using micromechanical finite element models. *Am J Phys Anthropol* 126:82-96.

Ryan TM and Walker A. 2010. Trabecular bone structure in the humeral and femoral heads of Anthropoid primates. *Anatom Record* 293:719-729.

Sarmiento EE. 1985. The evidence for terrestrial quadrupedalism in the hominid lineage. *Am J Phys Anthropol* 66(2)-224-225.

Sarmiento EE. 1998. Generalized quadrupeds, committed bipeds, and the shift to open habitats: an evolutionary model of hominid divergence. *American Museum Novitates* 3520:1-78.

Scherf H and Tilgner R. 2009. A New High-Resolution Computed Tomography (CT) Segmentation Method for Trabecular Bone Architectural Analysis. *Am J Phys Anthropol* 140:39-51.

Shea BT and Inouye SE. 1993. Knuckle-walking ancestors. *Science* 259:293-294.

Shaw CN and Ryan TM. 2012. Does skeletal anatomy reflect adaptation to locomotor patterns? Cortical and trabecular Architecture in human and non-human Anthropoids. *Am J Phys Anthropol* 147:187-200.

Smith RJ and Jungers WL. 2007. Body mass in comparative primatology. *J Hum Evo* 32:523-559.

Stern JT. 1975. Before bipedality. *Yrbk Phys Anthropol* 19:59–68.

Stern JT, Jungers WL, and Susman RL. 1995. Quantifying phalangeal curvature: an empirical comparison of alternative methods. *Am J Phys Anthropol* 97:1-10.

Straus WL. 1949. Riddle of man's ancestry. *Quarterly Rev Bio* 24:200-223.

Susman RL. 1979. The comparative and functional morphology of hominoid fingers. *Am J Phys Anthropol* 50:215-236.

Tague RG. 2002. Variability of metapodials in primates with rudimentary digits: *Ateles geoffroyie, Colobus guereza,* and *Peridicticus potto. Am J Phys Anthropol* 117:195-208.

Tuttle RH. 1967. Knuckle-walking and the Evolution of Hominoid Hands. *Am J Phys Anthropol* 26(2):171-206.

Tuttle RH. 1969. Knuckle-walking and the problem of human origins. *Science* 166(3908):953-961.

Tuttle RH. 1974. Darwin's apes, dental apes, and the descent of man: Normal science in evolutionary anthropology. *Current Anthropol* 15:389-398.

Tuttle RH. 1975. *Parallelism, brachiation, and hominid phylogeny*. In Phylogeny of the Primates: A Multidisciplinary Approach. (Eds. WP Luckett & FS Szalay) Plenum Press: New York. pp. 447-480.

Tuttle RH and Cortright GW. 1988. *Positional behavior, adaptive complexes and evolution*. In Orang-utan biology. (Ed. J Schwartz) Oxford Univ. Press: New York and Oxford. pp. 311-330.

Usherwood JR, Larson SG and Bertram JEA. 2003. Mechanisms of force and power production in unsteady ricochetal brachiation. *Am J Phys Anthropol* 120:364-372.

Vereecke E, Aerts P. 2008. The mechanics of the gibbon foot and its potential for elastic energy storage during bipedalism. *J Exp Bio* 211:3661-3670.

Vereecke E, D'Aout K, De Clercq D, Van Elsacker L, Aerts P. 2003. Dynamic plantar pressure distribution during terrestrial locomotion of bonobos (*Pan paniscus*). *Am J Phys Anthropol* 120:373-383.

Vereecke E, D'Aout K, Van Elsacker L, De Clercq D, Aerts P. 2005. Functional analysis of the gibbon foot during terrestrial bipedal walking: Plantar pressure distributions and three-dimensional ground reaction forces. *Am J Phys Anthropol* 128:659-669.

Waarsing JH, Day JS, and Weinans H. 2005. Longitudinal micro-CT scans to evaluate bone architecture. *J Muscoskeletal Neuro Inter* 5(4):310-312.

Washburn SL. 1967. Behavior and the origin of man. *Proc Royal Anthropological Institute of Great Britain and Ireland* 3:21–27.

Washburn SL. 1968. *Speculations on the problem of man's coming to the ground*. In Changing Perspectives on Man. (Ed. B Rothblatt) Univ. of Chicago Press; Chicago. pp. 193–206.

Williams SA. 2010. Morphological integration and the evolution of knuckle-walking. *J Hum Evol*. 58:432-440.

Wunderlich RE. 1999. Pedal form and plantar pressure distribution in anthropoid primates. Doctoral Dissertation, SUNY Stony Brook: New York.

Wunderlich RE & Jungers WL. 1998. Force distribution on the digits during knuckle-walking. *Am J Phys Anthropol* 26:236.

Wunderlich RE and Jungers WL. 2009. Manual digital pressures during knuckle-walking in chimpanzees (*Pan troglodytes*). *Am J Phys Anthropol* 139(3):394-403.

Youlatos D. 2002. Positional behavior of black spider monkeys (*Ateles paniscus*) in French Guiana. *Int J Primatol* 23(5):1071-1093.

Zeininger A, Richmond BG, and Gideon H. 2011. Metacarpal head biomechanics : A comparative backscattered electron image analysis of trabecular bone mineral density in *Pan troglodytes*, *Pongo pygmaeus*, and *Homo sapiens*. *J Hum Evol* 60:703-710.